XVII. *Further Observations on the Organization of the Fossil Plants of the Coal-Measures.*—Part III. Lyginodendron *and* Heterangium.

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[Plates 18–29.]

Contents.

	Page
Introduction	704
I. *Lyginodendron*	705
A. The Stem	705
1. General Structure	705
2. Course of the Vascular Bundles	707
3. Structure of the Vascular Bundles	711
4. The Secondary Tissues	714
5. The Pith and Pericycle	717
6. The Cortex	718
7. On certain small Stems of the *Lyginodendron* type	720
8. Structural anomalies	722
B. The Leaf.	725
1. Connection between Leaf and Stem	725
2. Form of the Leaf	726
3. Structure of the Petiole and Rachis	728
4. Structure of the Lamina	730
5. On a peculiar Bud-like Structure	732
C. The Root	733
1. Connection between Root and Stem	733
2. Primary Structure of the Root	736
3. Secondary Tissues of the Root	739
4. Branching of the Root	740
D. Habit and Dimensions of the Plant	741
II. *Heterangium*	744
Introduction	744
i. *Heterangium Grievii*	745
A. The Stem	745
1. General Structure	745

Page.
2. Course of the Vascular Bundles 747
3. Primary Structure of the Stele and Leaf-trace Bundles 748
4. The Secondary Tissues 751
5. The Cortex 753
6. Branching of the Stem 753
B. The Leaf 754
1. Connection between Leaf and Stem 754
2. Form and Structure of the Leaf 755
C. The Root 756
1. Connection between Root and Stem 756
2. Structure of the Root 758
D. Habit and Dimensions of the Plant 759
ii. *Heterangium tiliœoides* 760
iii. On a *Heterangium* of uncertain species 764
III. Affinities of *Lyginodendron* and *Heterangium* 765
Explanation of the Plates. 771

INTRODUCTION.

The two genera, *Lyginodendron* and *Heterangium*, are among the most interesting, and at the same time the most puzzling, representatives of the Carboniferous Flora. Although, unfortunately, we are still without any satisfactory evidence as to the nature of the reproductive organs in either genus, yet the structure of all their vegetative parts is preserved with such completeness and perfection as to enable us to show, that these fossils present a combination of characters such as exists in no group of plants now living. So long as the mode of reproduction is unknown, it will remain impossible to assign these genera definitively to their systematic position; in the mean time, we can only weigh with due care such evidence as is afforded by their vegetative structure. This evidence, as we shall show, clearly indicates, so far as it goes, a position intermediate between Ferns and Cycads.

At least two other fossil genera, *Poroxylon*, which was investigated by MM. BERTRAND and RENAULT, and *Protopitys*, our present knowledge of which is chiefly due to Count SOLMS-LAUBACH, appear to share this intermediate position.* Curiously enough, in these genera, also, the vegetative characters alone are known.

The further consideration of affinities will be postponed to the end of the paper, and we will now go on at once to consider the organization of *Lyginodendron*, which, of our two genera, appears to stand the nearer to Cycadeæ, though many of its characters are obviously Fern-like.

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* BERTRAND et RENAULT, "Recherches sur les Poroxylons," 'Archives botaniques du Nord de la France,' 1886.

SOLMS-LAUBACH, "Ueber die in den Kalksteinen des Kulm von Glätzisch-Falkenberg in Schlesien enthaltenen Structur-bietenden Pflanzenreste—II.," 'Botanische Zeitung,' 1893.

I.—LYGINODENDRON.

The history of this genus has been given in a previous memoir.[*] The fossil in question was first described by BINNEY, in 1866, under the name of *Dadoxylon Oldhamium*, was next transferred by WILLIAMSON, in 1871, to his genus *Dictyoxylon*, and was subsequently placed by him in GOURLIE'S genus *Lyginodendron*, previously known from cortical impressions only. *Lyginodendron* is now characterized by its structural features, which are quite distinct from those of any other genus. Its relation to the cortical impressions is a question of some difficulty, to which we shall return below (p. 741).

All the forms with which we are concerned may be provisionally referred to the same species, or rather type, namely, *Lyginodendron Oldhamium*. Its stems are among the commonest fossils preserved in the calcareous nodules of the coal-measures of Lancashire and Yorkshire, and they have also been found in those of Langendreer and Orlau, in Germany, but not, it seems, in any of the French coal-fields. The Sphenopteroid foliage of the plant is often found in association, and sometimes in connection, with the stem. The petiole is identical with the fossil formerly described as *Rachiopteris aspera*, as was shown in Memoir XVII., above cited. We have already recorded our discovery[†] that *Kaloxylon Hookeri* represents the adventitious roots of *Lyginodendron*. The evidence for these conclusions will be given in later paragraphs (see pp. 725 and 733).

The abundance of the material and its remarkably perfect preservation have placed us in a very favourable position for working out the structure, and have enabled us to distinguish characters which are constant and essential from mere individual peculiarities. Variations of the latter kind are rather frequent and include some interesting anomalies.

A.—THE STEM.

1. *General Structure.*

The stems, which we are about to describe, are of very variable dimensions. The smallest specimens do not exceed 3 millims. in diameter; the largest *undoubted* stem of *Lyginodendron* which we possess attained a diameter of about 4 centims. We leave out of consideration for the present both Mr. NEILD'S specimen[‡] and the cortical impressions. These must have belonged to stems of enormously greater size, but we cannot absolutely prove their identity with *Lyginodendron* (see below, p. 741).

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[*] WILLIAMSON, "Organization of the Fossil Plants of the Coal Measures," Part IV., 'Phil. Trans.,' 1873, p. 377.

The other memoirs of the series relating to *Lyginodendron* are: Part VI., 1874, vol. 164, Part II., p. 675 (*Rachiopteris aspera*, now known to be the petiole of *Lyginodendron*); Part VII., 1876, vol. 166, Part I., p. 1 (*Kaloxylon Hookeri*, now known to be the root of *Lyginodendron*); Part XIII., 1887, vol. 178, B., p. 289 (*Kaloxylon*); Part XVII., 1890, vol. 181, B., p. 89.

See also SOLMS-LAUBACH, "Fossil Botany," English translation, 1891, p. 358.

[†] WILLIAMSON and SCOTT, "The root of *Lyginodendron Oldhamium*," 'Roy. Soc. Proc.,' vol. 56, 1894.

[‡] See "Organization," Part IV., p. 386.

Full descriptions of the characteristic structure of the stem have been given in previous memoirs.* It will, however, be necessary to recapitulate what is already known, for our re-examination of the material, with the aid of additional specimens, has thrown new light on various points. Photograph 1, Plate 18, represents the transverse section of a stem of medium size which we may take as a typical example. This specimen, however (of which we have three sections), though unrivalled for the preservation of the most important details, is not so perfect, as a whole, as are some of the others. In fig. 1, Plate 21, a transverse section of another stem from an entirely new specimen is shown, the preservation of which is remarkably complete.

The middle of the central cylinder is occupied by a solid parenchymatous pith, imbedded in which are groups of dark sclerotic cells. At the periphery of the pith there are several distinct strands of primary xylem. Two of these, from the same specimen as photograph 1, are shown on a larger scale in Plate 21, figs. 2 and 3. Beyond the primary strands of xylem, we come to a broad zone of secondary wood, the elements of which are arranged with great regularity in radial rows. This secondary wood is divided up by numerous medullary rays, both primary and secondary.

If any doubt could be entertained as to the mode of development of the woody zone, it is removed by the fact that at its outer limit the cambium itself is often preserved in great perfection (see Plate 22, fig. 7).

On its outer side the cambium is continuous with a zone of thin-walled tissue, which is made up of phloëm-groups, separated from one another by the phloëm-rays. The greater part of this layer is secondary, as is shown by the radial seriation of its elements. On its external border, however, the primary phloëm-groups can still sometimes be recognized (see Plate 21, fig. 1, and Plate 22, fig. 7, *ph.*). The phloëm-zone is again surrounded by a ring of thin-walled tissue, which is best regarded as a pericycle (see Plate 22, figs. 5, 6, and 7). Imbedded in this we find groups of the same somewhat sclerotic cells, which are so conspicuous in the pith. At the exterior of the pericycle there is usually a layer of periderm.

Beyond the periderm we come to the cortex proper. Its inner zone is usually the worst preserved part of the specimen. Only fragments of it are present in the specimen shown in Plate 18, photograph 1; in the stem represented in the drawing, Plate 21, fig. 1, it is better preserved. The inner cortex consists of large-celled parenchyma, among which numerous sacs (probably secretory) are scattered.

The outer cortex is made up of the well-known alternate radial bands of sclerenchymatous fibres and parenchyma, forming what is termed by Count SOLMS-LAUBACH the *Dictyoxylon* cortex.† As has often been described, the sclerenchymatous strands anastomose in the tangential direction, forming long meshes, which are occupied by the parenchyma. Beyond the sclerenchymatous zone, there are a few more layers of parenchyma more or less imperfectly preserved. The epidermis itself is never perfect and has generally been destroyed.

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* WILLIAMSON, "Organization," Parts IV. and XVII.

† "Fossil Botany," p. 7.

One of the most important features remains to be mentioned, namely, the so-called cortical vascular bundles. These are in reality the leaf-traces on their way out to the petioles; their true nature was pointed out in a previous memoir,* and additional evidence is brought forward in the present paper (see Plate 18, photographs 3 and 4, and Plate 23, fig. 10). In most specimens, including those shown in photograph 1 and fig. 1, five of these leaf-traces are present in the transverse section; the majority of these traces are double, forming the "twin-bundles" so characteristic of the plant. All these bundles are imbedded in the pericycle, a position which they maintain until they turn out into the leaf-bases. The innermost bundles constantly possess a fan-shaped mass of secondary xylem and phloëm on their outer side.

The above may suffice for a summary of the more obvious points of structure in a typical stem of *Lyginodendron*. In order to gain a more complete conception of the anatomy, the first thing necessary is to obtain a clear knowledge of the course and structure of the primary vascular bundles. To this subject we have devoted special attention, and we will take it first in our more detailed survey.

2. *Course of the Vascular Bundles.*

In considering the distribution of the primary vascular tissues of the stem we have to determine the course of the cortical bundles,† and of those which lie at the periphery of the pith, and to trace the relation between the two systems. The former are complete bundles with both xylem and phloëm (see Plate 22, figs. 5 and 6); the latter are xylem-strands only, for their phloëm has been removed towards the outside by the intercalation of the secondary tissues. That the cortical strands are leaf-traces has already been proved; we shall endeavour to demonstrate below, that the perimedullary strands are simply the lower internal portions of the same leaf-trace system, thus confirming a conjecture of Count SOLMS-LAUBACH'S.‡ First of all, however, it is necessary to determine with greater exactness the course of the bundles in the cortical region, and their relation to the leaves. These points are best studied by the comparison of transverse sections. Longitudinal sections are obviously necessary as auxiliaries, but the leaf-traces pass out so very gradually, that it is never possible to follow their whole course in any one preparation.

In any good transverse section through an internode, we see that the external bundles lie at somewhat different distances from the centre of the stem. Thus in

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* WILLIAMSON, "Organization," Part XVII., p. 90, 1890.

† The external bundles are conveniently spoken of as *cortical*, though we more usually find them within the limits of the pericycle.

‡ "Fossil Botany," English edition, p. 360.

Plate 21, fig. 1 the relative position of these bundles is evident and is indicated by numbers, *l.t.*^{1} being the most internal, and *l.t.*^{5} the most external of the five leaf-traces.

The innermost leaf-trace, *l.t.*^{1}, is still within the general contour-line of the secondary wood, while *l.t.*^{2} has only just passed beyond it. Both these traces are solitary bundles, and each has a secondary arc, which is more developed in *l.t.*^{1} than in *l.t.*^{2}. The next outer trace, *l.t.*^{3}, is already double, and has no secondary tissues; *l.t.*^{4} is similar, but lies a little further out, while *l.t.*^{5} is still nearer the periphery. This last trace, like the rest, is within the pericycle, which, however, here shows a marked outward protrusion. It will be noticed that, behind each of the four inner strands, there is a gap in the secondary wood occupied by parenchyma, while, behind the outermost leaf-trace, *l.t.*^{5}, this gap has already been filled up by intercalated secondary tissues. We will speak of this gap as the *trace-gap.*

The order of the outgoing bundles can be traced in a similar manner in the stem shown in Plate 18, photograph 1. The same general rules hold good for all transverse sections, where the preservation is sufficiently perfect.

We now have a number of specimens showing the leaf-trace bundles actually passing out into the base of the leaf. Previous figures (Part IV., Plate 16, fig. 25; and Part XVII.,* Plate 12, fig. 1) show the twin bundles in transverse section as they traverse the cortex and enter the leaf-base. Plate 18, photograph 3 and Plate 23, fig. 10 in the present paper represent two transverse sections from the same specimen showing a petiole in connection with the stem. The vascular bundles have here passed out so far as to belong definitively to the petiole. In Plate 18, photograph 4, a corresponding radial section from another specimen is shown. Here the foliar vascular bundle can be traced from the pericycle of the stem, through the cortex, and can be followed for a long distance in the petiole itself.

There is in the WILLIAMSON collection a series of eight successive transverse sections from the same stem.† Considerations of space have prevented us from figuring the series, which throws great light on the course of the vascular bundles. The lowest section shows the base of a petiole attached to the stem, and a second petiole makes its appearance towards the upper end of the series, which thus extends through one internode. The divergence between these two successive leaves is $\frac{2}{5}$, and this seems to have been the most usual phyllotaxis in *Lyginodendron*. The trace, which passes out into the upper of the two leaves, can be followed throughout the series; it is a double bundle all through this part of its course. In the sixth section from below it begins to bend out into the leaf-base, and, as it does so, its two bundles unite somewhat, forming a V with the angle outwards; this very frequently happens at the base of the petiole, though sometimes the bundles remain quite distinct (see

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* These references are to the WILLIAMSON Memoirs fully cited above (p. 705, footnote).

† C.N. 1191–1198. The proper order of these sections *from below upwards* is as follows: C.N. 1198, 1192, 1193, 1194, 1195, 1197, 1196, 1191.

Plate 18, photographs 3 and 5, and Plate 23, fig. 10; *cf.* Part VI., Plate 52, fig. 6; Part XVII., Plate 13, fig. 2).

Another point of great interest is shown by the same series; the *innermost* of the leaf-traces shown is, at the bottom of the series, deeply imbedded in the secondary wood. In the next section it has passed a little way out, and its position and structure are almost exactly similar to those of the bundle (from another stem) shown in Plate 22, fig. 5. As we trace it further up, we find that its secondary wood gradually disappears. At the top of the series the strand, which now consists of primary tissues only, has become a double bundle, similar to that shown in fig. 6. Hence we may infer that, roughly speaking, the change of structure shown by the comparison of figs. 5 and 6 is gone through in about one internode. This is confirmed by the fact that the bundles shown in those two figures, both of which belong to the same transverse section,* are separated by a divergence of $\frac{2}{5}$.

In the series C.N. 1198–1191 only four cortical traces are present in each transverse section of the internode, because one trace has passed out at the bottom of the series and is not replaced until the next node is reached. More usually five such traces are seen in any transverse section of an internode, as shown in photograph 1 and in fig. 1.

The following conclusions may be drawn from the facts brought forward, which are supported by confirmatory evidence from numerous specimens:

1. The phyllotaxis is spiral, and the divergence (except in very small stems) $\frac{2}{5}$.
2. As a rule each trace passes through five internodes between entering the pericycle and bending out into a leaf.
3. In its course through the lowest of the five internodes the trace usually loses its secondary arc of tissue, and begins to divide into two bundles.
4. The now double trace continues its course with but little change through the remaining four internodes, but passes very gradually outwards, the pericycle bulging somewhat to make room for it.
5. Ultimately it becomes free from the pericycle, and passes out through the cortex into a petiole, where its two bundles often become partially reunited.

As each internode must have been, as our specimens show, at least an inch long, it is evident that the outward passage of the leaf-traces must have been exceedingly gradual. The trace turned out rather sharply, however, where it entered the leaf, as shown in Plate 18, photograph 4.

The nature of the "cortical bundles" and their relation to the leaves is thus made clear; we have now to consider their relation to the internal xylem-strands.

The number of these strands, as seen in transverse section, is more variable than that of the external bundles. We usually find five of the latter, never more. The internal bundles also often number five (see Plate 18, photograph 1), but are sometimes more numerous, the maximum number observed being eight, as shown in Plate 21, fig. 1. Where their number is equal to that of the cortical bundles, they alternate quite regularly with the latter, as shown in photograph 1.* Where they are more numerous, we find the reason is, that certain of the single medullary bundles are replaced by a pair (see Plate 21, fig. 1). The alternation, however, is always preserved.

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* As a matter of fact they were drawn from two *adjacent* sections, between which there is no appreciable change of structure.

That the medullary bundles are continuous with the cortical leaf-traces is proved by the fact that we often find bundles in the intermediate position, in the act of passing out from pith to pericycle. If, as is almost always the case, the stem possesses secondary tissues, the bundle is here enclosed by the secondary wood, which has formed on its outer side only, while behind it is a parenchymatous gap (see Plate 23, fig. 9). We find examples of these transitional bundles in all positions between pith and pericycle. In the case figured the bundle is scarcely half-way out. On one side its own cambium is continuous with that of the rest of the cylinder. On the other side the main cambium bends inward. In Plate 21, fig. 1 a corresponding bundle, *l.t.*[1], is shown a little further out. Here the general cambium has already formed behind it. In the series C.N. 1198–1191 already referred to, a bundle can be traced all the way from near the pith into the pericycle. At the top of the series another bundle is just beginning to pass out from the pith.†

The identity of the medullary and cortical bundles is further proved by the study of very young stems (which are rare), such as that of which a transverse section is shown in Plate 18, photograph 2. Here only three or four layers of secondary wood have been formed. Consequently, there is comparatively little separation between the medullary and cortical bundles. Four cortical traces are shown, the fifth appears to have passed out into a petiole. The innermost cortical trace, namely, that which has not yet split into two bundles, is only just free from the ring of wood. There are six medullary bundles, which alternate (either singly or in pairs) with those of the cortex. The study of this section at once shows that cortical and medullary strands are identical bundles cut through at different parts of their course, and thus confirms the evidence obtained from more advanced stems.

We may, therefore, draw this further conclusion, as to the course of the vascular bundles in the stem: the medullary bundles form the downward continuation of the xylem-strands of the same leaf-traces which pass out through the cortex into the leaves. The question now arises, How do the bundles behave on entering the pith, and how is the alternation of the medullary and cortical strands to be accounted for? The evidence on this point is imperfect, but certain indications are afforded by the comparison of transverse sections. In the series so often referred to (C.N. 1198–1191) a bundle is shown in the uppermost section just entering the pith. As we trace it downwards, it appears to attach itself to one of the adjacent medullary strands, namely that on the kathodic side. Unfortunately the preservation of this part is not good enough for the course of this bundle to be followed with absolute certainty.

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* This fact was already recorded in "Organization," Part IV., p. 383.

† C.N. 1191. See also C.N. 1140 and C.N. 1190, 1138, and 1885 E.; the three last form a series from below upwards.

One point, however, throws considerable light on this question. If we determine the outermost leaf-trace in any transverse section, we know that its place will be taken a little higher up the stem by a bundle passing out from the pith. Consequently it is from the medullary bundles adjacent to the gap corresponding to this leaf-trace, that the next cortical strand will be supplied. Now, we often find that this gap has a double bundle on its kathodic and a single one on its anodic side (see Plate 18, photograph 1, *l.t.*^{5}; the kathodic medullary bundle is shown in Plate 21, fig. 3, the anodic in fig. 2; see also fig. 1, *l.t.*^{5}).

If, however, we examine a bundle, which is already passing out through the wood, we find that the medullary strands on either side of it are both single bundles. All this points to the conclusion that a leaf-trace, when followed downwards into the pith, turns aside and joins the next medullary strand on its kathodic side.

If this were all, it would involve the fact that each medullary strand is a sympodial bundle, built up of the lower parts of all the leaf-traces of one orthostichy. It is, however, more probable that connections also take place in the opposite direction, for it is not likely that the bundle system of each orthostichy was quite isolated from the rest. The frequent occurrence of double medullary bundles in other positions than that already determined (see Plate 21, fig. 1) perhaps points to the existence of these additional fusions.

In any case, we may safely draw the following general conclusion as to the course of the vascular bundles: the bundle-system in the stem of *Lyginodendron* is entirely a leaf-trace system. The longitudinal course of each leaf-trace extends through at least ten internodes, about five of which are passed through in the cortex and pericycle, and the same number at the outside of the pith.

The medullary strands are thus sympodial bundles formed of the united lower portions of the adjacent leaf-traces.

The general similarity to the bundle-system of *Osmundaceæ* is evident.*

3. *Structure of the Vascular Bundles.*

There can be no question that the vascular bundles in the stem were of *collateral* structure. This is most certainly shown by the medullary strands, which consist solely of xylem elements, abutting directly on the cells of the pith. There is no trace of phloëm on their inner side, and the preservation is often so perfect as to make it certain that no elements have been lost (see Plate 21, figs. 2 and 3, transverse, and Plate 22, fig. 4, longitudinal). The phloëm of these bundles has been entirely displaced towards the exterior owing to the interposition of secondary wood by the cambium. In good preparations the group of primary phloëm belonging to each medullary xylem strand can be clearly recognized at the corresponding point of the phloëm-zone (see Plate 21, fig. 1 and Plate 22, fig. 7, *ph.*).

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* See DE BARY, "Comparative Anatomy of Phanerogams and Ferns," English translation, p. 280. The similarity is not diminished by the more recent observations of ZENETTI, 'Bot. Zeitung,' 1895, p. 53.

The leaf-traces in the external part of their course demonstrate the same fact. Although there is small-celled tissue on the internal side of the bundle, yet the more delicate phloëm (Plate 22, fig. 6, *ph.'*) is perfectly distinct and is evidently limited to the outer side of the xylem. The collateral structure is equally evident in bundles in the intermediate position, which have a cambial arc of their own. Here there is secondary as well as primary phloëm, both of which are found on the external side of the bundle only (see Plate 22, fig. 5, *ph.''*, also Plate 23, fig. 9). Longitudinal sections of the outgoing bundles afford confirmatory evidence.*

In the petiole, as we shall see more fully below, the structure of the bundles becomes *concentric*. It is a question of considerable interest, at what point this important change of structure takes place. It is not easy to answer the question with absolute accuracy, for it is only in the best preserved sections that the position of the phloëm, as distinguished from mere small-celled parenchyma, can be determined with certainty. This much, however, is clear: so long as the outgoing bundles remain in the pericycle of the stem they maintain a collateral structure; on the other hand, when they have definitely entered the leaf-base they are certainly concentric. Thus, in our Plate 21, fig. 1, the four traces, marked *l.t.*^{1}–*l.t.*^{4}, consist of purely collateral bundles; the outermost trace, *l.t.*^{5}, which is already bulging the pericycle, shows some signs of an encroachment of the phloëm on the inner edge of the xylem-groups.

The double bundle in the base of the leaf, shown in Plate 18, photograph 3 and Plate 23, fig. 10, is distinctly concentric. The change then takes place in the region, where the bundle passes out through the cortex to enter a leaf-base.†

We have next to consider in detail the structure of the xylem of the primary bundles. We will begin with the medullary strands, which, as we have seen, simply represent the leaf-traces in the lower part of their course. The inspection, even of transverse sections alone, at once reveals a characteristic feature; the smallest elements of the xylem lie neither at the outer nor inner edge, but are placed in an intermediate position, nearer the outer than the inner surface. This statement holds good without exception for all the very numerous transverse sections investigated. A few typical instances are shown in the illustrations (see Plate 18, photographs 1 and 2, and more especially Plate 21, figs. 2 and 3, and Plate 23, fig. 8). The smallest xylem-elements are accompanied by a few parenchymatous cells; the surrounding xylem is entirely composed of tracheæ. The similarity to the xylem of a bundle in the leaf of a Cycad at once suggests itself. Longitudinal sections justify the comparison, for they prove that the small xylem-elements are spiral tracheæ, which thus constitute the *protoxylem* or first-formed elements of the primary wood (see Plate 22, fig. 4, which represents a radial section, passing through a primary xylem-strand, bordering on the pith). It will be seen that the tracheides to the exterior of the protoxylem are scalariform, while those on its inner side are pitted. There is a sharp distinction between the primary xylem and the tracheides of the secondary wood. The structure described remains constant throughout the stem. The position of the protoxylem is maintained, as the bundle passes out from the pith (see Plate 23, fig. 9) and remains the same after it has reached the pericyle (see Plate 22, figs. 5 and 6). It cannot be too strongly emphasized, that the protoxylem does not lie on the limit of the primary and secondary wood, but is placed in the interior of the primary strand itself, so that the development of the primary wood must have been partly centripetal and partly centrifugal. This fact is well illustrated by fig. 6. The leaf-trace shown in that figure has reached a point on its outward course where secondary wood is no longer formed, yet the position of the protoxylem in the interior of the ligneous strand is quite obvious. That the centrifugal wood to the outside of the protoxylem is not secondary but primary, is proved, both by the irregularity of its arrangement, as shown in transverse section (see figs. 2, 3, 5, 6, and 8), and also by the character of the markings on its walls (see fig. 4). The limit between the centrifugal primary wood and the true secondary wood with radially arranged elements is perfectly sharp (see figs. 2, 3, 4, 5, and 8). In many cases the two are actually separated by parenchymatous cells.

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* *E.g.*, C.N. 1982, from which photograph 4 is taken.

† These statements are based on the comparison of many sections, among which the following may especially be mentioned, in addition to those figured for this purpose: C.N. 1144 D., 1190, 1191–1198, 1640, 1885 G.

We are convinced that the same interpretation holds good for the foliar bundles of Cycadeæ, and that here also the centrifugal part of the wood must be regarded as a primary structure, though in certain cases it may receive subsequent additions from a cambial layer.

We regard then the structure of the vascular bundles in the stem of *Lyginodendron* as identical with that of the foliar bundles of Cycadeæ.

This type of structure has been called *diploxylic*, but this term is so used by MM. BERTRAND and RENAULT[*] as to imply that the centrifugal part of the wood is secondary. We may either coin a new term, and call bundles in which the protoxylem lies in the interior of the primary strand of wood *mesoxylic*, or adopt the word *mesarch*, suggested by Count SOLMS-LAUBACH.[†] The stem-bundles then of *Lyginodendron*, like the leaf-bundles of Cycadeæ, are *mesarch* or *mesoxylic*[‡] in structure.

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[*] "Faisceaux foliaires des Cycadées actuelles," 'Archives Bot. du Nord de la France,' 1886.

[†] "Fossil Botany," p. 257. The term *mesarch*, which has the advantage of being the shorter, implies that the development *begins* in the *middle* of the strand of wood.

[‡] This new term corresponds to the terms *perixylic* and *centroxylic* used by M. VAN TIEGHEM, the former term implying that the protoxylem is peripheral, the latter, that it is directed towards the centre of the stem. In *mesoxylic* bundles the development of the primary wood is partly centripetal, partly centrifugal.

As regards the number of protoxylem-groups in each bundle, we usually find one such group in each strand in the medullary part of its course (see Plate 21, fig. 2), except at places where there has been a fusion of strands.

As a bundle leaves the pith on its outward course, its protoxylem soon becomes doubled (see Plate 22, fig. 5 and Plate 23, fig. 9). Where the leaf-trace first divides into two bundles, each has a single protoxylem-group (see fig. 6). Further out towards the leaf these again double (see Plate 21, fig. 1, *l.t.*^{3}, *l.t.*^{4}, and *l.t.*^{5}).

In the medullary part of its course the xylem of the bundle contains little or no parenchyma, except that adjoining the protoxylem-elements (see figs. 2, 3, and 8). Further out, the amount of parenchyma in the xylem becomes greater and it is not always limited to its original position. The only other change which need be mentioned is that in the outer part of the course of a bundle, scalariform or densely spiral tracheæ become more numerous in comparison with the pitted elements (see Plate 23, fig. 13, which is from a petiole). This change begins within the stem.

As regards the primary phloëm of the vascular bundles there is, as might be expected, little detail to be given. The large groups, lying in the pericycle immediately opposite the medullary strands of woods (see Plate 21, fig. 1 and Plate 22, fig. 7, *ph.*) are in some cases surprisingly well preserved, and must have contained elements more resistant than those of the secondary phloëm, though the thickness of the cell-walls is not sufficient to justify one in speaking of them as hard bast. Secretory sacs occur in the primary phloëm, as well as in the other soft tissues of the plant. Longitudinal sections passing through the phloëm of leaf-trace bundles, sometimes show the structure tolerably well. We find a combination of elongated elements, with oblong parenchymatous cells, and may conjecture that the former were the sieve-tubes (see fig. 13, *ph.*, from a petiole).

The conclusions at which we have arrived respecting the structure of the primary bundles of *Lyginodendron* may be stated as follows : 1. The vascular bundles in the stem are normally collateral. As they pass out into the leaves, however, their structure becomes concentric. 2. The xylem of the bundles in the stem developed like that of the foliar bundles in Cycadeæ. The protoxylem-elements lie in the interior of the primary wood, but nearer its outer surface. Thus, the greater part of the primary xylem was centripetally developed, while a smaller portion was centrifugal. 3. The primary xylem consisted of spiral, scalariform, and pitted tracheides, together with a little parenchyma. 4. The primary phloëm consisted of sieve-tubes and parenchyma, together with secretory sacs.

4. *The Secondary Tissues.*

With the rarest exceptions all known stems of *Lyginodendron* already possess secondary tissues. The young stem, represented in transverse section in Plate 18, photograph 2, shows the structure at a very early stage. Similar specimens have been observed with little or no secondary wood, but these are always in a somewhat fragmentary condition.

That the zone of wood and bast, superadded to the primary bundle system, was really of a secondary character, is conclusively proved by well-preserved specimens in which the actual cambium is often quite evident (see Plate 18, photograph 1, Plates 21 and 22, figs. 1, 5, and 7). It is also manifest that the cambium was a normal one, forming wood on its inner and bast on its outer surface. We leave out of consideration for the moment certain individual anomalies, which we shall describe below (p. 722).

The cambial cells, which form the xylem and phloëm elements, were of the usual tabular form, as seen in transverse section (see fig. 7). In the development of the medullary rays the tangential divisions were no doubt less frequent, for the cambial cells in this region have a greater radial diameter. The general character of the secondary growth resembles that of the stem in the Cycads.

In the very young stem, shown in photograph 2, it will be noticed that the thin zone of secondary wood, whether fascicular or interfascicular, is of about the same thickness all round the stem. It evidently formed, from the first, a continuous ring, only interrupted at the point of exit of a leaf-trace bundle. Hence we must infer that the interfascicular cambium began its activity almost simultaneously with that in the bundles themselves (see also photograph 1 and fig. 1).

It is clear that the cambium followed the course of the outgoing bundles for some little distance, for these bundles have their own arcs of secondary wood and bast up to a certain point in their outward course. The secondary arc dies out as we trace the bundle upwards (see Plates 21–23, fig. 1, $l.t.^1$ and $l.t.^2$, figs. 5 and 9). Below this point, however, the cambium has already closed in behind the outgoing bundle, so that for a certain distance there is a double layer of cambium. There is the special arc of cambium belonging to the leaf-trace bundle itself (fig. 5, $cb.''$), and, besides this, there is the general cambium, which is continuous behind it. The parenchyma, occupying the gap behind the leaf-trace bundle, where the cambium had not yet closed in (see figs. 1 and 9), followed the secondary growth by dilatation, accompanied, no doubt, by irregular cell-divisions. Some curious anomalies which appear in this region are described below (p. 723).

The whole secondary zone is made up of radiating laminæ of xylem and phloëm, with medullary rays between. We see no reason for departing here from the usual terminology, which would be applied without hesitation to the stems of Cycadeæ, the plants which most nearly resemble *Lyginodendron*, so far as the secondary tissues are concerned.

The primary medullary rays usually became divided up at once by the formation of interfascicular laminæ of wood and bast (see photographs 1 and 2, fig. 1, &c.).

Conversely the wood and bast, which are formed opposite the primary bundles, are from their first origin subdivided by secondary rays (see figs. 2 and 3). Additional secondary rays appear *de novo* in the later-formed layers, as secondary growth proceeds (see fig. 1, &c.). The proportion of rays to wood and bast varies much in different specimens, and in different parts of the same specimen. On the whole, the interfascicular wood is richer in ray-tissue than the fascicular, but this is not a constant rule. All the medullary rays are continuous through the cambium into the phloëm, so that we can speak of xylem-rays and phloëm-rays just as in the case of recent trees (see Plate 22, fig. 7).

The structure of the secondary wood is excessively simple; it consists of tracheides and ray-parenchyma only. The tapering ends of the tracheides can often be clearly seen, and sometimes it is evident that the pits are closed throughout, so that we have direct evidence that the xylem elements were really tracheides, and not vessels (see Plate 22, fig. 4B). The tracheides are of great length, but we have not attempted measurements, as we could not make sure of following the same element throughout its whole length.

The tracheides have very numerous pits, which usually, if not always, are limited to their radial walls. The pits are crowded together, and as many as seven longitudinal rows may exist on the same wall. They show signs of an arrangement in inclined series, as if they formed part of a spiral system. The pits are distinctly bordered, as can be seen both in tangential and radial sections. The opening of the border is a wide inclined slit; the pits between tracheides and ray cells are, as usual, unbordered on the side towards the latter (see figs. 4A and 4B).

The rays are of very variable height and width; their cells are decidedly thin-walled, and consequently are only well-preserved in good specimens. They are radially elongated, and thus show in radial sections the muriform appearance characteristic of most medullary rays in recent plants.*

The cells with dark carbonaceous contents, which we interpret as secretory sacs, and which are so general in all parenchymatous tissues of *Lyginodendron*, frequently occur in the medullary rays.

The secondary phloëm has a very characteristic structure; it is divided up into small groups corresponding to the tracheal groups in the wood, and separated from one another by the parenchymatous phloëm-rays (see Plate 22, fig. 7 and 7A). In each radial series of phloëm elements, there is a regular alternation of larger and smaller cells (see fig. 7). The tangential section appears to show that the smaller elements of the phloëm were rather elongated, with occasional transverse walls, while the larger elements had oblique terminations. Great caution, however, is necessary in interpreting the structure, on account of the presence of articulated fungal hyphæ in the partially disorganized phloëm (see fig. 7A).

The preservation does not allow us to say for certain which are the sieve-tubes. We think it most likely that the larger elements were of this nature, while the narrower cells were parenchymatous. The analogy of *Heterangium tiliæoides*, in which the phloëm is perfectly preserved, supports this view. MM. Bertrand and Renault however, have come to the opposite conclusion in the case of *Poroxylon*, the phloëm of which much resembles that of *Lyginodendron*.*

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* See WILLIAMSON, "Organization," Part IV., Plate 23, fig. 9; also our fig. 4.

The medullary rays broaden out somewhat in passing through the phloëm zone. The secretory sacs are more frequent here than in the xylem portion of the rays (see figs. 1, 5, and 7). Occasionally the medullary rays of the wood show signs of tangential dilatation, owing perhaps to the long-continued growth of the pith, but this is exceptional.

We may sum up our results as to the secondary tissues in the stem as follows: 1. The stem of *Lyginodendron* constantly formed a large amount of secondary wood and bast by means of a normal cambial layer. 2. The secondary wood consisted of tracheides and xylem-rays; the former possessed numerous bordered pits on their radial walls. 3. The secondary bast-zone consisted of groups of phloëm separated by the phloëm-rays. In the phloëm larger and smaller elements alternated regularly. It is probable, though not certain, that the larger elements were the sieve-tubes. 4. The secondary tissues bear a general resemblance to those in the stem of Cycadeæ.

5. *Pith and Pericycle.*

The pith of *Lyginodendron* consists of moderately thin-walled parenchyma, in which large groups or nests of dark-coloured tissue are imbedded. These almost black masses, which also occur in the pericycle, and sometimes in the cortex, give a most characteristic appearance to the sections (see photographs 1 and 4, fig. 1, &c.). It is not easy to determine the nature of the tissue of which they are composed. The cells in question do not differ greatly in form from those of the thin-walled medullary parenchyma. Their walls, however, are decidedly thicker and their arrangement is more regular, showing a fairly definite longitudinal seriation. Their cavities are more or less completely filled with carbonaceous contents. It is a question whether these carbonaceous bodies represent the actual contents of the cells or whether they are due to the degradation of the inner layers of the much thickened cell-walls. We incline to the latter view: (1) because the apparent contents often show a distinctly laminated structure and (2) because the fibres of the outer cortex, which were certainly sclerenchymatous, are often filled with similar material. We will, therefore, provisionally speak of the dark-coloured groups as the *sclerotic nests*.

The pith further contained numerous thin-walled sacs, with more uniform carbonaceous contents, which we regard as probably of a secretory nature. They are sometimes isolated, sometimes arranged in vertical rows (see Plate 21, figs. 2 and 3, also Plate 25, fig. 19, in which the same organs are shown in the cortex of a root). These organs are of universal occurrence, throughout the soft tissues of *Lyginodendron*, and may even be found within the limits of the vascular bundles. In a previous memoir* these structures have been described and figured as *gum-canals;* on careful examination, however, we have failed to find any good evidence of an epithelium, while in satisfactory longitudinal sections, transverse or oblique walls, separating the constituent cells, can generally be detected (see fig. 19). We therefore prefer to describe all these organs as secretory sacs. It is useless to speculate on the question what they secreted.

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* 'Recherches sur les *Poroxylons*,' *loc. cit.*, p. 289.

Certain regions of the pith evidently retained the power of meristematic activity for some time, as is proved by the anomalous tissues to which they occasionally gave rise (see p. 722). Through the trace-gaps the pith is perfectly continuous with the pericycle. Where a bundle leaves the pith on its outward course, it is constantly accompanied by some of the sclerotic nests (see figs. 1 and 9); similar nests, however, are also frequent in the pericycle without special relation to the bundles.

The pericyclic tissue consists, like the pith, of rather delicate, short-celled parenchyma, together with sclerotic nests and numerous secretory sacs (see photograph 1 and figs. 1, 5, 6, 7, and 9). The pericycle is often of great thickness, especially at the point where a leaf-trace is approaching its place of exit into a leaf (see photograph 4 and fig. 1).

In all except the youngest stems the pericycle is bounded externally by a zone of radially arranged cells which we interpret as *periderm* (see photograph 1, and figs. 1, 5, 6, 7, and 9, *pd.*). This layer, which was evidently formed from a phellogen, appears not to have originated until secondary growth had made some progress. In a stem with secondary wood about twelve elements thick the first tangential divisions had taken place in the outer layer of the pericycle.† The outer elements of the radially arranged zone have somewhat thick walls, while its inner cells are quite delicate, and no doubt constituted the cork-cambium or phellogen (see figs. 5, 6, and 7). It is natural to suppose that this periderm must have ultimately caused the throwing off of the whole cortex, but we have no direct proof that this took place. The periderm curves outwards opposite the leaf traces, following their outer surface. In the specimen shown in photograph 4, the periderm extends along the external surface of the outgoing trace as far as the base of the petiole. The length of the peridermal cells, as shown in longitudinal sections, is about equal to their tangential diameter.

6. *The Cortex.*

The cortex, as distinguished from the pericycle, may be divided into two layers. The inner layer is parenchymatous, while the outer consists of alternating radial bands of sclerenchyma and parenchyma, constituting the characteristic *Dictyoxylon* cortex, as it is called by Count SOLMS-LAUBACH. The cortex may be passed over in few words, as its structure has been sufficiently described in former memoirs. It must, however, be pointed out that "the inner parenchyma of the bark," described in Memoir IV., p. 382, includes both phloëm and pericycle, in addition to the inner cortex of our present description. The specimens discovered up to 1872 were not sufficiently well preserved for all the zones to be distinguished.

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* WILLIAMSON, "Organization," Part XVII., p. 90, Plate 12, fig. 4.

† C.N. 1915 H.

The inner cortex presents little of interest; it is generally the worst preserved part of the stem, although its cells had somewhat thicker walls than those of the pericycle. Its frequent disorganization in specimens otherwise perfectly preserved (see Plate 18, photograph 1) may be an indication that it had begun to die off in consequence of the formation of internal periderm while the plant was still living. For the structure of this layer, see Plate 21, fig. 1, and Plate 18, photograph 4. In some of the specimens many of the cells seem to have collapsed, giving the appearance of a tissue with larger elements than actually existed.*

The secretory sacs are specially abundant in the inner cortex. We rarely find sclerotic nests in this region except at the bases of leaves, where they are very numerous (see Plate 18, photographs 3 and 4, and Plate 23, fig. 10), and whence they extend into the cortical tissue of the petiole. As regards the outer cortex the only point which need be mentioned is the great tangential dilatation of the parenchymatous bands, owing to the secondary growth in the interior of the stem (see photograph 1 and fig. 1). This dilatation, which reaches its maximum in the outer cortex, applies to all regions external to the cambium. In some cases it is very conspicuous in the pericycle, where it sometimes leads to a wide separation between the two bundles of a leaf-trace. Secretory sacs occur in the parenchymatous portions of the outer cortex. As already mentioned, a few layers of tissue are sometimes preserved to the exterior of the "*Dictyoxylon*" zone. The remarkable outgrowths or emergences which arise on the outer surface of the cortex have been fully described and figured in Part XVII., Plate 12, figs. 1 and 6. They each consist of a sclerotic envelope enclosing a parenchymatous core, these two tissues being continuous with the corresponding parts of the external cortex. The apex of the outgrowth is blunt. The emergences (for they are certainly too deep-seated to be called hairs) are by no means equally frequent in all the specimens; in many cases they probably became detached, together with the superficial cortical layers. Very similar appendages are found on some recent tree-ferns, as *Alsophila armata*, and more especially *Alsophila australis*, in which the blunt spines are much like those of *Lyginodendron*. In these ferns the spines are surmounted by paleæ, which soon become detached, but whether this was the case in *Lyginodendron* also cannot be determined.

The emergences have played an important part in the scientific history of the plant, for it was the identity of these structures on the stem of *Lyginodendron* and on the petiole known as "*Rachiopteris aspera*" which first suggested that these organs might be different parts of one and the same plant—a suggestion which has been amply confirmed since by their discovery in direct continuity.*

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* See WILLIAMSON, "Organization," Part XVII. Plate 13, fig. 3.

7. *On certain Small Stems of the* Lyginodendron *type.*

In a previous memoir attention has been called to the peculiarities of certain very small stems which, from their general structure, appear to belong to *Lyginodendron.*† At that time the *roots* of *Lyginodendron* were not yet understood; it now turns out that the smallest of the supposed stems, including all those with the "central axis solid," were really roots. This applies to the following specimens, enumerated on p. 94 of the memoir cited: C.N. 1885 C., 1885 A., 1883 and 1885.

There remain, however, a certain number of very small true stems, the nature of which is proved beyond doubt by the presence of leaf-trace bundles in their cortex. Examples of such stems are shown in figs. 11 and 12 of Part XVII., and in fig. 2 of Part IV.

A clear distinction must be drawn between those *small* stems which differ in their primary structure from the typical forms, and merely *young* stems, which are characterized simply by the absence or small development of the secondary tissues. One of these young stems is shown in transverse section in photograph 2, and has been already mentioned (pp. 710 and 714). Here there is a well-marked pith, and the bundles surrounding it are distinctly separated from one another. Other examples at about the same stage of growth are known, some of which are of considerable size. They present no special difficulties, being evidently stems of the normal type at an early stage of development. In these young specimens the outer cortex is mainly sclerenchymatous, with only narrow radial bands of parenchyma. The great development of the latter in older stems was, no doubt, largely due to dilatation induced by the secondary growth.

Returning to the stems in which the primary structure is on a small scale and is peculiar in type, we may distinguish two categories. The one is represented by fig. 2 in Memoir IV. and fig. 11 in Memoir XVII., the other by fig. 12 in Memoir XVII. In the former type the primary xylem forms an almost complete ring, or, at least, is not differentiated into distinct bundles; in the second type, the bundles surrounding the pith are quite distinct and normal, but the whole is on an extremely small scale. In fact, the smallest stems we have, one of which is only 3 millims. in diameter, belong to this type. These smallest stems have secondary wood of considerable thickness (about 14 cells thick). Cambium and phloëm are well preserved, and the leaf-traces are evident in the cortex. The phyllotaxis appears to have been $\frac{1}{3}$. In one of the specimens the outer cortex is of the normal "*Dictyoxylon*" type, with the parenchymatous bands already dilated. On the whole, we may say that these tiny stems have all the characteristic structure of *Lyginodendron*, except that the sclerotic nests are absent.*

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* WILLIAMSON on "Organization," Part IV., p. 405; Part VI., p. 682; Part XVII., p. 91.

† WILLIAMSON, "Organization," Part XVII., p. 92.

The small stems of the type with an almost continuous ring of primary wood (see Memoir XVII., fig. 11) are never quite so minute as those just described, the smallest found having a mean diameter of barely 4 millims. (C.N. 1137). The structure only differs from that of the typical *Lyginodendron* stem in having a continuous xylem-ring and a very small pith. Specimens of this kind are connected by an unbroken series of intermediate forms with the typical stems, which have a large pith with separate bundles at its periphery. These differences are quite irrespective of the amount of secondary thickening, and therefore cannot depend on the *age* of the branch. It might be easy to explain them as dependent on the *order* of the branch, but we have at present no evidence, that the stem of *Lyginodendron* branched at all. It may have done so, but not a single branching specimen has yet been detected. The supposed branches mentioned in earlier memoirs have all turned out to be either roots or petioles. We are, therefore, not justified in assuming the presence of a highly developed system of ramification such as would be necessary to account for the existence of branches of various orders.

The explanation we would suggest is, that the small specimens, with a continuous ring of primary wood, may represent the *basal, first developed* portions of normal stems.

Osmunda, as is well known, resembles *Lyginodendron* in the fact that the normal stem possesses a ring of collateral bundles, which are distinct, so far as their xylem is concerned. M. LECLERC DU SABLON in his interesting memoir on the development of the stem in Ferns, has shown that the lower internodes of the stem of *Osmunda* have a continuous ring of wood enclosing the small pith, this ring being only interrupted at the nodes. It is only in the later-developed part of the stem that the pith enlarges and the bundles become permanently distinct.†

A similar stage is passed through by the stems of many other ferns. Until we have been able to trace the transition in one and the same stem of *Lyginodendron* from the small pith and continuous xylem of the basal portion to the large pith and separate bundles of the upper stem, our suggestion must remain an hypothesis. In the mean time, however, it may serve as a provisional explanation, which is in harmony of what we know of the development of those recent Ferns which in their anatomy most nearly resemble our fossil. The fact that *Lyginodendron* had secondary growth in thickness, while the Ferns with which we have compared it have not, does not invalidate the comparison. We have good reason to believe that the secondary thickening in *Lyginodendron* and its allies was relatively a recently-acquired character. It is highly probable that they still retained the mode of growth characteristic of plants which are destitute of secondary thickening. In like manner *Dracæna* or *Aristea* resembles any other Monocotyledon in the earlier stages of its development though it ultimately forms secondary tissues.*

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* See C.N. 1139 and 1141 (same specimen), 1199, and especially 1885 D.

† LECLERC DU SABLON, "Recherches sur la formation de la tige des Fougères," p. 9, figs. 25 and 26, 'Ann. des Sci. Nat. (Bot.),' sér. 7, vol. 11, 1890.

The very small stems with a normal pith and separate bundle (see "Organization," Part XVII., Plate 14, fig. 12) remain unexplained. They are not connected by any clear intermediate forms with the typical specimens, yet it is impossible to doubt that they belong to *Lyginodendron*. Their xylem elements are decidedly smaller than those of the ordinary stems, but the latter vary so much among themselves in this respect, that we cannot attach much importance to such differences. Stems of this kind must apparently represent some kind of lateral axis, which has not yet been found in connection with the main stem. The somewhat deficient formation of sclerenchyma suggests that they may have been weak runners or subterranean shoots.

8. *Structural Anomalies.*

So far we have concerned ourselves with the normal structure of the *Lyginodendron* stem, such as is common to a majority of the numerous specimens investigated. Some interesting departures from this typical anatomy occur in individual specimens. The most remarkable and perhaps the most frequent of these anomalies depended on the appearance of a secondary meristem at the outer border of the pith. In some stems this medullary meristem gave rise merely to secondary parenchyma, with somewhat thickened walls; in other cases, however, it acted as a regular cambium, producing medullary wood and bast with inverted orientation. In the latter case, we have precisely the same anomaly as in *Tecoma*, *Iodes*, or *Acantholimon* among recent plants. It is a most remarkable fact, that this peculiarity should have already appeared as an *occasional variation* in a carboniferous plant, so absolutely remote from the Dicotyledons as is *Lyginodendron*. A more striking warning against the *indiscriminate* use of, even conspicuous anatomical characters cannot be imagined. Such a warning, it is true, is not needed by those who have experience in anatomy. The anomaly in question is known to be of very inconstant occurrence at the present day. Both in the genera, *Tecoma* and *Iodes*, some species show it and others do not, though analogous peculiarities (internal phloëm for example) are often characteristic of entire natural orders. Anatomical characters, in fact, like any other characters, are sometimes of great constancy, sometimes highly variable, while the same character, which is relatively constant in one family may be most inconstant in other groups.

In the present paper, we have been compelled, in the absence of organs of fructification, to make great use of anatomical characters. We have, however, endeavoured to rely on those which are known to be of great persistency in families which presumably belong to the same cycle of affinities as the plants with which we are dealing.

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* The following slides show a more or less continuous xylem-ring:—C.N. 1137, 1150 ("Organization," Part IV., Plate 22, fig. 2); 1161, 1885 H ("Organization," Part XVII., Plate 13, fig. 11); 1915 N, 1915 R.

Characters dependent on the activity of the cambium are perhaps peculiarly liable to variation. Whenever a plant has acquired the power of secondary tissue-formation, all the anomalies, even of the most abnormal Dicotyledons become possible; in *Lyginodendron* some of these possibilities are actually realized.

We do not find the slightest reason to believe that the anomalous medullary cambium of *Lyginodendron* was a character even of specific value; among stems, which are perfectly similar in other respects, some show it and some do not, while in those that possess this anomaly, the degree in which it is developed is most variable.

A characteristic example of the formation of anomalous medullary wood and bast has been previously figured.*

Our fig. 8 (Plate 23), from another section of the same stem, shows plainly that there is a true cambium on the medullary side of the primary bundles, giving rise to secondary xylem on its outer side, and to secondary phloëm towards the interior. The figure cited from Memoir XVII. demonstrates an interesting point, confirmed by other specimens, namely, that the anomalous medullary tissues extend through the leaf-trace gap along the sides of the normal secondary wood. In the section from which this figure was drawn, the zone of secondary wood is sub-divided by parenchymatous trace-gaps into four masses, each of which is completely surrounded by cambium. We have, in fact, in this case precisely the anomaly described by DANGEARD in *Acanthophyllum*.† It is probable that the new cambial divisions spread from the normal cambium through the parenchyma of the leaf-gaps into the pith, just as ROBINSON found to be the case in *Iodes tomentella*.‡ Thus in another stem, from which fig. 9 was drawn, there is a small amount of anomalous wood (x^3) behind the outgoing trace figured. The anomalous tracheæ found at the edges of the leaf-trace gaps sometimes have a horizontal course ("Organization," Part XVII., Plate 13, fig. 3).

In one or two instances, where the anomalous tissue is mainly parenchymatous, the internal cambium appears to have arisen partly from the parenchyma of the primary xylem, so that some of the tracheæ belonging to the latter have been carried inwards into the pith.§ We omit one or two specially complicated forms of anomalous medullary tissues, which are of isolated occurrence.||

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* "Organization," Part 17, Plate 13, fig. 3. The cabinet contains four sections of this specimen, C.N. 1138, 1142, 1190, and 1885E.

† DANGEARD, "Monographie Anatomique des *Acanthophyllum*;" 'Le Botaniste,' 1889.

‡ ROBINSON, "On the Stem-structure of *Iodes tomentella*, &c.," 'Annales du Jardin Botanique de Buitenzorg,' vol. 8, 1890.

§ C.N. 1114 and 1118. One of us found a similar mode of development in *Acantholimon* (see SCOTT and BREBNER "On Internal Phloëm in the Root and Stem of Dicotyledons," 'Annals of Botany,' vol. 5, 1891, p. 296.)

|| The following specimens in the WILLIAMSON collection show anomalous tissues in the pith: C.N. 1114, 1118, 1138 and other sections of the same stem; 1153.

Other individual anomalies are connected with the leaf-trace bundles in the outer part of their course. In most cases the secondary tissues only accompany the outgoing trace so long as it remains undivided; sometimes, however, both the twin bundles of a divided trace possess an external layer of secondary wood and bast.* In another case we found one bundle of a pair unthickened, while its twin developed an enormous fan of secondary tissue with wood about 40 cells thick (C.N. 1114). A more remarkable anomaly of rather rare occurrence consists in the formation of cambium all round the leaf-trace bundle instead of on the peripheral side only. An instance of this is shown in the first figure of *Lyginodendron* published.† In another stem both the twin bundles of a divided leaf-trace showed the same peculiarity on a still larger scale, while another pair approached the same structure. In these cases the thickened bundle acquires a concentric structure, and may easily be mistaken for the stele of a branch, as actually happened in the first instance referred to. These pericyclic anomalies sometimes coexist with abnormal formations in the pith. In one case, a little nest of sclerotic cells in the pericycle had served as a centre for a concentric development of anomalous xylem and phloëm, similar to that around the leaf-trace bundles. These varied eccentricities of development are only of interest, as showing the same plasticity of structure in these ancient stems as we find in so many modern plants, which resemble them in nothing except their mode of secondary growth. The anomalous developments in certain Cycadeæ, among which we should most naturally look for parallel cases, bear only a remote resemblance to those which we find in *Lyginodendron*.‡ The concentric cortical strands which are formed in *Cycas* appear to be of purely secondary origin.

Frequent peculiarities, scarcely amounting to an anomaly, consist in the differentiation of the normal secondary wood into distinct zones, chiefly differing in the dimensions of their tracheides. When a narrow zone of small tracheides is formed with large elements on both sides of it, an appearance suggestive of annual rings may result. These phenomena, however, are far too inconstant for us to draw any inference as to a regular periodicity of growth. It is much more probable, that the differences between successive zones of wood, which only appear in certain individual stems, were due to some accidental interference with the normal course of development. Examples of these peculiarities have been previously figured.§

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* See Plate 2, photograph 8, also WILLIAMSON, Part IV., Plate 22, fig. 1; Plate 25, figs. 19 and 20.

† WILLIAMSON, Part IV., Plate 22, fig. 1.

‡ See DE BARY, 'Comparative Anatomy,' Eng. edition, pp. 608–613.

§ See WILLIAMSON, Part IV., Plate 22, fig. 4; Plate 23, fig. 6.

B.—THE LEAF.

1. *Connection between Leaf and Stem.*

The history of our knowledge of the leaves of *Lyginodendron Oldhamium* is briefly as follows: In Memoir IV. (1872) the opinion was already expressed that the "small stems or petioles" to which the provisional name of *Edraxylon* had been given, might probably prove to belong to *Lyginodendron* (*loc. cit.*, p. 403). In Memoir VI., the specimens first named *Edraxylon* are fully described, and are incorporated in the provisional genus *Rachiopteris* (founded for the reception of fossil fern-petioles) under the name of *R. aspera.* The structure is fully described, and the discovery of leaflets in connection with the branched petiole, led to the conclusion that the leaf belonged to BRONGNIART'S genus, *Sphenopteris.* The species *S. Hœninghausi,* which agrees with *R. aspera* in possessing a tuberculated rachis, was specially suggested for comparison.

At a later period[*] the conclusion "that *Rachiopteris aspera* is merely the petiole of *Lyginodendron Oldhamium*"[†] was definitely stated, and proved by specimens in which the base of the petiole was found in actual connection with the stem, as well as by the presence of identical cortical outgrowths on both organs.

It only remains for us to call attention to some additional specimens, in which the connection between leaf and stem is still more manifest. Two of these new specimens have been figured.

Photographs 3 and 8A and fig. 10 (Plates 18, 19, and 23) are from the same specimen, of which we have four transverse sections.[‡] The order of the sections illustrated, from below upwards, is photograph 3, fig. 10, photograph 8A. In all the sections figured the petiole is in manifest continuity with the stem, and, at the same time, it already presents the characteristic structure of *Rachiopteris aspera.* Other sections show the same petiole after it has become free; thus, fig. 11 represents the upper part of the same petiole in longitudinal section, at a point where it is beginning to branch. This figure shows several of the characteristic cortical emergences, thus affording the direct proof that *Rachiopteris aspera,* the only known *Rachiopteris* that possesses these outgrowths, was the petiole of *Lyginodendron.*

Photograph 4, from another specimen, shows a radial section through a stem bearing a petiole. Both are in admirable preservation, so that all the details of the leaf-base can be made out. We also have series of sections from two other specimens, showing the connection between stem and petiole, and also the structure of the petiole after it has become free, where it presents all the characteristics of *Rachiopteris aspera.* *

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[*] See WILLIAMSON, Part XVII., 1890.

[†] *Loc. cit.*, p. 91.

[‡] C.N. 1980 and 1981, and two sections in the possession of D. H. SCOTT. All these were cut by Mr. LOMAX, as well as those mentioned in the next foot-note. Other slides belonging to these series are in the Botanical Collections of the Royal College of Science, London.

The leaf is attached to the stem by a massive base, which, however, is not at all sheathing (see photographs 3 and 4, fig. 10). The leaf-trace bundles, which had traversed the pericycle almost vertically through about five internodes, bend out somewhat sharply into the base of the leaf (see photograph 4). It has already been mentioned that the bundles, which are collateral in the stem, become concentric as they enter the leaf. The extent to which the two bundles of the trace fuse on entering the petiole varies in different specimens; in that represented in fig. 10 they partially fuse; in other cases (*e.g.*, C.N. 1984) they remain distinct. All the primary tissues, vascular bundles, pericycle, inner and outer cortex are, as we should expect, perfectly continuous between stem and leaf. The limit between cortex and pericycle is, however, difficult to trace at the point of junction. The sclerotic nests, which in the stem are almost always limited to the pericycle, become distinctly cortical in the petiole, forming a conspicuous feature which helps to characterize the species.†

There is always a great development of these sclerotic masses in the axillary region, a fact which is worth noticing because these conspicuous groups of cells might be mistaken for rudimentary axillary buds. We find no evidence that such buds existed.

Exactly below the axil a characteristic transverse hypodermal band of black sclerotic tissue is found (see photograph 4 and fig. 10). This helps us to fix very exactly the position of the transverse as compared with the longitudinal sections of the node. The outer cortex of the stem closes in again almost immediately above the level of the sclerotic band.

The subject of phyllotaxis has already been dealt with. The arrangement is evidently $\frac{2}{5}$ in all the larger stems, in which the relative position of the leaf-trace bundles is clear. In the smallest stems the divergence seems to have been $\frac{1}{3}$.

2. *Form of the Leaf.*

This subject was discussed in Memoir VI., at a time when the relation of *Rachiopteris aspera* to *Lyginodendron* had not yet been determined.

The stems of *Lyginodendron* are almost invariably found to be surrounded by a multitude of fragments of foliage, among which petioles of all sizes, often in the act of branching, are to be recognized, as well as portions of leaflets. Wherever the structure is sufficiently well preserved, the characters of *Rachiopteris aspera* are evident in the petioles, as indicated by the V- or W-shaped bundle as seen in transverse section, the Dictyoxylon cortex and the peculiar emergences. Sometimes, of course, there is an accidental admixture of other fern petioles.

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* C.N. 1983 and 1984; also three sections from this series in the possession of D. H. Scott.

Numerous single sections in the Williamson collection also show the connection between petiole and stem, as C.N. 1140, 1144 B, 1144 D, 1190, 1191 and 1198 (two nodes of the same stem), 1885 G, 1915 C.

† See Williamson, Part VI., p. 682.

In all cases where the petioles can be determined as belonging to *Rachiopteris aspera* we now know that we have to do with the foliage of *Lyginodendron.* The finer branches of these petioles, as was already shown in Memoir VI., are sometimes found in connection with portions of the compound lamina. Where the latter are seen in surface view, some idea of the form of the leaf may be obtained. Since Memoir VI. was published, additional evidence has been accumulated, and the conclusion then reached is confirmed, namely, that the leaf would fall under the form-genus *Sphenopteris* of BRONGNIART, as shown by the finely cut foliage and the acute angles between the veins.* It is impossible to reconstruct the leaf from the fragmentary remains, which are alone available: but we may take it as certain that it was a highly compound leaf of the *Sphenopteris* type. The leaflets appear to have been decurrent on the finer branches of the rachis. We cannot venture to refer the leaf to any known species of *Sphenopteris,* but a certain resemblance to various forms can be traced. (See, for example, the figures of *S. Hœninghausi, S. tridactylites, S. linearis,* &c., in BRONGNIART'S "Histoire des végétaux fossiles.")

The mere fact, that the foliage of *Lyginodendron* resembled that of certain Ferns is in itself no proof of affinity with *Filices.* The classical case of *Stangeria* is a sufficient warning against any such hasty inference. It must, however, be remembered that in the foliage of *Lyginodendron* we have not only fern-like *form* and venation, but also fern-like *structure,* whereas in the case of *Stangeria* a single transverse section of the petiole would be sufficient to prove that the plant is no Fern but a Cycad.

Where a number of sections have been cut from the same specimen, it is possible to trace the repeated branching of the rachis and to observe the insertion of the leaflets upon its branches. The leaflets shown in section in Plate 19, photograph 7, and Plate 24, fig. 16 are from the series C.N. 1191–1198, and belong to leaves, the petioles of which, seen in other sections of the same series, present the characteristic structure of *Rachiopteris aspera.* A section of one of the petioles from this series, no doubt a secondary branch, has been figured in Memoir XVII., Plate 13, fig. 7. Though not actually one of those which have been traced up to the leaflets, it is identical with them in structure, and most probably formed part of the same compound leaf. These leaflets and branch petioles accompany the stem, which, as already mentioned, runs through the entire series. They, no doubt, belong to a lower leaf than the two which are seen in connection with the stem.

The section shown in Plate 18, photograph 6, evidently passed through a portion of the lamina, just where the segments are beginning to separate from one another. Appearances of this kind are not uncommon in the preparations, and become readily intelligible on comparison with the surface view of the foliage (*cf.* Memoir VI., Plate 52, fig. 15).

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* See Memoir VI., Plate 52, fig. 13; also Memoir XVII., p. 91.

The following conclusions as to the form of the leaf may be drawn from our observations:—

1. The leaf of *Lyginodendron* was a highly compound one, the branches of the rachis being given off alternately.
2. The form and venation of the leaflets were those of a *Sphenopteris*.*

3. *Structure of the Petiole and Rachis.*

This again is a subject which has been so fully dealt with in previous Memoirs, that only a few points need be discussed here.

None of the preparations hitherto figured afford conclusive evidence as to the structure of the vascular bundle. We will, therefore, first call attention to Plate 18, photograph 5, which shows a petiole in transverse section; from its small size—2 millims. in maximum diameter—it no doubt represents one of the ramifications of the main petiole. The preservation is remarkably perfect, in fact, scarcely a cell is lost. The concentric structure of the bundle comes out with astonishing clearness, which could not be exceeded in a preparation from a recent Fern. The small celled, thin-walled tissue constituting the phloëm is absolutely perfect and completely surrounds the V-shaped xylem. The maximum thickness of the phloëm-zone is found on the convex or morphologically lower side of the bundle; it thins out somewhat at the lateral angles, and again attains a considerable thickness on the concave upper face. The larger thin-walled cells bordering on the cortex are best regarded as pericycle. Neither here nor in any other specimen, do we find any differentiated bundle-sheath or epidermis; considering the perfection of the preservation we are probably justified in concluding that in *Lyginodendron*, as in the Marattiaceæ of the present day, a specialized endodermis was not developed. Secretory sacs are scattered among the phloëm-elements.

Every well-preserved transverse section of a petiole shows the same fact, that the bundle was concentric Where two bundles are present, as usually happens in main petioles, and sometimes in their secondary branches, each bundle is surrounded by its own zone of phloëm, except where the two are on the point of fusing (*cf.* Memoir XVII., Plate 13, fig. 2). Longitudinal sections confirm these conclusions.†

The position of the spiral tracheides or protoxylem in the petiolar bundle is not always easy to determine in the transverse sections, but with the help of the longitudinal sections this can be done. There were always several such groups. Thus, in the specimen shown in photograph 5, there were certainly three, one near the bend at the middle of the xylem and one near each end; in larger bundles they were more numerous. The smallest elements were not situated at the periphery of the xylem, but were imbedded in its mass, nearer the lower than the upper surface. That the elements in question are really the spiral tracheides or protoxylem is proved by the longitudinal sections (see Plate 23, fig. 13, *px.*, *cf.* also C.N. 1982).

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* The following are the most important specimens which throw light on the form of the leaf:—C.N. 134, 135, 137, and 139; these four form a series; 143, 147; 1191–1198, a series; 1855, 1856, 1885D, 1979.

† See especially C.N. 1978 and 1985; from the latter, fig. 13 was drawn. Both these sections are from petioles found in actual continuity with the stems of *Lyginodendron*. For additional good transverse sections of petioles, *cf.* C.N. 139, 146, 1194, 1854, 1857, 1984.

We thus see, that the position of the initial strand is essentially the same as in the bundles of the stem. We desire to call special attention to the fact that there is not the slightest reason for regarding the *centrifugal* or lower portion of the xylem in the leaf* as secondary, which is the view of MM. BERTRAND and RENAULT in the case of *Poroxylon*. In *Lyginodendron* this tissue shows no sign of radial seriation and consists mainly of spiral or reticulate elements, while pitted tracheides chiefly occur in the centripetal portion of the xylem. In *Poroxylon*, true secondary wood was no doubt formed in the leaf, but we do not feel certain from the figures that there may not have been some *primary* centrifugal wood here also.†

The wood of the petiole resembles the primary wood of the stem except that it has a larger proportion of spiral and reticulated as compared with pitted elements. A certain amount of thin-walled parenchyma was present among the tracheides. It is probable that a layer of parenchyma also separated the tracheides from the phloëm.

The phloëm, as seen in longitudinal section, consists of very elongated elements, probably the sieve-tubes, and of shorter parenchymatous cells (see fig. 13, *ph.*).

The great point to be emphasized as regards the bundles in the petioles of *Lyginodendron* is, that they are the typical concentric bundles of a Fern, whereas those in the stem have a distinctly Cycadean character.

We have preferred to use the old term *concentric bundle* rather than *stele* in this case, because the vascular tissue of the petiole forms the direct continuation of the collateral strands of the stem, which no one could regard as anything else than vascular bundles of the usual type.

The inner cortex of the petiole presents one or two points of interest. It is traversed longitudinally by great numbers of those elongated tubes with carbonaceous contents which we regard as being of the nature of secretory sacs. The individual sacs must have been of great length in the petiole, for their terminal walls are rarely met with. They sometimes anastomose with one another, but we cannot say whether an actual fusion ever took place. The cortical parenchyma is crossed in a horizontal direction by transverse bands of short sclerotic cells. These often form, together with the longitudinal secretory organs, a most conspicuous network.‡ It is doubtful, however, whether the two kinds of elements really had any special relation to one another, though, on the other hand, it is possible that some of the cells at the edges of the sclerotic bands may themselves have been of a secretory nature.*

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* In every petiole of *Lyginodendron* the upper and lower side can easily be determined in any transverse section. The upper side is flat or concave, the lower side is convex. The form of the bundle or bundle-pair follows the same rule (see Memoir VI., figs. 1, 6, 7, Memoir XVII., Plate 13, fig. 7, also our photographs 3 and 5 and fig. 10).

† See BERTRAND and RENAULT, 'Sur les *Poroxylons*,' figs. 219, 220.

‡ Something is shown of this on a small scale in fig. 11. This and many other anatomical details could not be adequately figured without increasing the number of illustrations beyond all bounds.

The outer cortex has the familiar "*Dictyoxylon*" structure, consisting of alternate radial strands of sclerenchyma and parenchyma. On its outer surface are seated the curious emergences to which the specific name of "*Rachiopteris aspera*" owed its origin. As a rule, they are quite similar to those borne on the stem, but sometimes the outer sclerenchymatous layer is less developed and may appear merely as a thick-walled epidermis (see Memoir XVII., in which fig. 6 should be compared with fig. 7). The form of these protuberances is somewhat variable; usually they are bottle-shaped. Count SOLMS-LAUBACH† speaks of them as *winged ribs*, an expression which might convey the idea that they are longitudinal ridges, of which the figures cited show the cross sections. This, however, is not the case. The petioles, it is true, are often somewhat winged on their upper edges, but such wings are quite distinct from the emergences, which may arise from any part of the surface. That they are not wings is shown by the fact that in a series of sections of the same petiole, their position never remains constant. Further evidence as to their real form is afforded by the fact that in longitudinal sections their appearance is essentially the same as in transverse section (see Memoir XVII., fig. 8), and also by the fact that the cross section of the emergence itself is circular (*loc. cit.*).

We have figured a peculiar form of these emergences, which is not unfrequently met with (see Plate 23, fig. 12). The emergence has the usual thick-walled superficial layer; its internal parenchyma is generally thin-walled, but near the free extremity, there is a sharply defined group of well-preserved cells, with strongly marked walls and brown contents. This group appears to be limited externally by a somewhat flattened layer of cells. The structure certainly suggests a *gland* of some kind. In several cases, even when there was no such well-defined mass of specialized cells, the appearance of the parenchyma in the emergence is that of a tissue, which had been rich in cell contents. It is quite possible that a glandular function may have been discharged in certain cases by these emergences.

4. *Structure of the Lamina.*

Hitherto nothing has been known as to the histological structure of the leaflets of *Lyginodendron*. Now, however, we have several sections which show the tissues in great perfection. Two such sections are represented in Plate 19, photograph 7, and Plate 24, fig. 16. Both are from the series C.N. 1191–1198 so often referred to, and form part of leaves, the petioles of which show the characteristic structure of

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* For the sclerotic bands, see "Organization," Part VI., Plate 52, figs. 11 and 12.

† "Fossil Botany," p. 361.

"*Rachiopteris aspera.*" We therefore know that these leaflets really belonged to our plant. Specimens in which such details of the leaf-structure are well preserved, are necessarily rare.

A vertical section such as those represented, shows first of all, that the structure of the lamina was distinctly bifacial or dorsiventral. Towards the upper convex surface of the leaflet, the mesophyll consists of closely packed cells, elongated at right angles to the surface. Towards the lower concave surface, the cells, though still somewhat elongated, become more irregular, are sometimes branched, and leave considerable intercellular spaces between them.

Where the section passes through a vascular bundle, we see that the latter is enclosed within a very definite parenchymatous sheath, consisting of large cells elongated parallel to the bundle. We have endeavoured to find out whether the fine bundles of the lamina are concentric or collateral, a question of considerable difficulty. In one or two cases we have seen that the spiral tracheides, of which the xylem is exclusively composed, are in direct contact with the bundle sheath on the side towards the upper surface of the leaf, while on the lower side some intermediate thin-walled elements could be recognized (see fig. 16; C.N. 1856 shows this point well). Most probably the bundles of the lamina were collateral, as in recent Ferns, though throughout the rachis they were certainly concentric. The tracheæ became dilated in some cases towards the ends of the veins. This dilatation may have been connected with the presence of a water-gland.*

We were unable to determine the position of the protoxylem in the vascular bundles of the lamina.

The leaf possessed a distinct hypodermal layer beneath the epidermis of the upper surface (see photograph 7 and fig. 16). The epidermis itself is not so well-preserved as the mesophyll, but in one or two places the stomata can be recognized. The clearest is seen in sectional view in fig. 16A. Here there seems to be no doubt, that we have the two guard cells (*g.c.*), lying at the base of a depression formed by the prominent subsidiary cells. We have so far found no trace of stomata on the upper surface of the leaf.

The lamina of the leaf occasionally has outgrowths on its lower surface, similar to those on the petiole and stem (see photograph 7 and fig. 16). It is a curious fact, that in the best sections of the leaf, almost every cell contains a round mass of carbonaceous matter, very suggestive of a nucleus. We do not desire to lay any stress on this appearance, but its constancy in the best preserved preparations is certainly remarkable. (See photograph 7 and fig. 16.)

The following conclusions result from our observations :—

1. The lamina of the leaf in *Lyginodendron* had a distinctly bi-facial structure with well differentiated palisade and spongy parenchyma.

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* C.N. 1856. See POIRAULT, "Recherches sur l'anatomie des Cryptogames vasculaires," 'Ann. des Sci. Nat.,' Bot., Sér. 7, t. 18, 1894.

2. The finer vascular bundles were probably collateral.
3. There was a hypoderma towards the upper surface *

5. *On a Peculiar Bud-like Structure.*

Before leaving the subject of the foliage, we wish to call attention to a very peculiar and indeed unique structure, which is represented in Plate 24, figs. 14 and 15. The organ at first sight strongly suggests the idea of a cone, and therefore attracted our special attention in the hope that we were at last on the track of the long-sought fructification of *Lyginodendron*. Subsequently, however, we found reason to give up this idea. The organ consists of an axis, imperfectly preserved in our specimen, which is densely clothed with prominent appendages, bearing a close resemblance to the well-known cortical emergences of the stem and leaf of *Lyginodendron*. The appendages are elongated and somewhat tapering; each has an envelope of sclerenchyma which becomes solid at the top. The central tissue is parenchymatous and has often perished, leaving a hollow. In no case is there any trace of a vascular bundle in an appendage. The transverse sections of the appendages are more or less semicircular near the base, becoming circular in their free part.

The axis of the whole structure, where it is cut radially, is found to be hollow (see fig. 14). In one of the sections the surface of the axis is shown in tangential view, and is seen to be marked with a number of patches of lighter coloured parenchyma, which no doubt represent the bases of as many appendages (see fig. 15). Between the parenchymatous areas the superficial tissues of the axis appear to have been fibrous, but the preservation is very imperfect.

We have two sections of this curious object. The extreme length of the whole structure is 14 millims., but it is doubtful whether the whole of this belongs to one specimen. The continuous portion represented in figs. 14 and 15 is only 4 millims. long.

We have rejected the idea of this specimen being a cone for two reasons :—

1. The appendages show no trace of vascular tissue, and therefore could hardly have been either sporophylls or sporangiophores of any kind, while on the other hand they agree exactly with the cortical emergences of *Lyginodendron*.
2. There is no trace of sporangia in connection with the organ.

The evidence for the specimen belonging to *Lyginodendron* at all depends solely on the structure of the appendages, the identity of which, with the cortical outgrowths of that plant, can scarcely be doubted, if, for example, our figures 14 and 15 be compared with Memoir XVII., Plate 12, fig. 6.

The explanation we would suggest is, that the structure represents either a bud or more probably a very young leaf covered with protective appendages of the nature of paleæ. The paleæ, or at least their bases, have remained, while most of the delicate young tissue of the organ which they protected has perished, leaving a hollow in the axis of the whole structure. The specimen is so remarkable, that we considered it worth figuring and describing, though its nature must at present remain problematical.

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* The best preparations for showing the structure of the leaflets are: C.N. 1196, and others of the same series, 1856, 1885 D, and 1979.

C.—The Root.

1. *Connection between Root and Stem.*

We have already briefly recorded our discovery that *Kaloxylon Hookeri* was the root of *Lyginodendron Oldhamium.*[*] We will now bring forward the evidence on which this conclusion is based.

It has long been known that the stem of *Lyginodedron* bore appendages quite distinct from the petioles. Several examples of these are described and figured in Memoir IV., p. 387, figs. 11, 12, 14, 16, 22, and 24. The appendages in question are shown passing out more or less horizontally from the wood, and traversing the cortex. They were at that time regarded as branches, though another specimen—which was really, no doubt, of the same nature—was already recognized as being probably a root (*loc. cit.*, fig. 7).

A number of better preserved specimens also showing these organs in connection with the stem have since been obtained. These afford evidence—

1. That the appendages in question were of endogenous origin, and presented in all respects the characteristic structure of roots.

2. That these roots are identical with the fossil previously described as *Kaloxylon Hookeri*.

We will first state the facts which prove that the appendages are morphologically roots.

Adventitious roots, with the rarest exceptions, are of endogenous origin ; they arise from deep-seated tissues (pericycle or endodermis), and have to grow out through the cortex of the parent stem. Hence they are readily distinguished from stem-branches, which are almost always of exogenous origin, arising from superficial tissues. A section of the cortex of the parent stem, passing through the base of an adventitious root, will show the latter as a complete organ, possessing a cortex and epidermis of its own ; a corresponding section at the base of a branch would show only the vascular tissues, which connect the bundles of the branch with those of the stem.

We have the clearest evidence that the appendages of the *Lyginodendron* stem were of the former kind. Plate 19, photograph 8, represents part of a transverse section of a large stem. An appendage, which evidently made a sharp bend close to its base, is shown in approximately transverse section in the inner cortex of a stem. Its vascular cylinder, which had undergone considerable secondary thickening, is surrounded, except on the inner side, by its own cortical zone, which is sharply marked off from that of the stem itself. At the same time, owing to the curvature of the organ, the connection of its xylem with that of the parent axis is clearly shown. Some of the tracheæ, which are here seen in longitudinal section, are continuous with those of the secondary wood, while others extend inwards as far as the primary xylem of the stem; the latter, however, is somewhat crushed.

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[*] ‘Proc. Roy. Soc.,’ vol. 56, 1894. [Mr. T. Hick arrived independently, and almost simultaneously, at the same conclusion, but solely on the evidence of comparative anatomy. See ‘Mem. and Proc. Manchester Lit. and Phil. Soc.,’ ser. 4, vol. 9, Session 1894–5. (D. H. S., Dec. 14, 1895.)]

Photograph 9 is from a tangential section of another stem, and here the appendage is shown passing though the outer or "*Dictyoxylon*" cortex. On the right a leaf-trace bundle on its way to a leaf is shown. Here again the transverse section of the appendage is evidently that of a root. The solid vascular cylinder, with its well developed secondary wood, is enclosed within a cortex of its own. It will be noticed that, in this instance, the appendage is passing out horizontally, which is the more usual case. The appendage is slightly compressed laterally, owing to the limitation of its growth by the sclerenchymatous strands of cortex through which it had to pass. The same phenomenon is observed in the adventitious roots of the Marattiaceæ—in which, however, the growth is, of course, primary only.

In photograph 10 another of these organs is shown from the same preparation. It is just becoming free from the cortex of the stem, a portion of which is shown to the right; the appendage still retains its compressed form, due to cortical pressure. The interesting point is, that it is itself beginning to branch. The two branches shown in the section have all the appearance of rootlets. The central cylinder has a primary mass of xylem without pith, and possesses abundant secondary wood; the cortex is well preserved, its large-celled outer layers are especially evident. In Plate 19, photograph 8A, another of these appendages is shown in longitudinal section (the stem being cut transversely), passing out from the wood, through the whole thickness of the cortex. We do not think that any botanist will hesitate, from the evidence already brought forward, in regarding these appendicular organs as *adventitious roots*, the name by which we shall henceforth call them.

Another specimen affords in some points still more conclusive proof of the nature of these organs. In this case we have three successive sections of the same specimen. Two of these sections are figured (Plate 25, fig. 18 and fig. 18A). They pass obliquely through a stem of *Lyginodendron*, and at the same time show several of the roots. In fig. 18 two of the roots shown (*rt.* 1 and *rt.* 2) are quite free, and remain so throughout the series. Two other roots (*rt.* 3 and *rt.* 4) are shown in transverse section, so far as their central cylinders are concerned. These roots, however, are curved, so that the section passes tangentially through a portion of the cortex of each, and shows that it is continuous with the *Lyginodendron* stem. The cortex of root 3 can be traced right through the outer cortex of the stem. Towards the interior, a portion of the vascular tissue of the root is also shown in longitudinal section A fifth root is seen exactly at its junction with the wood of the stem. It may be mentioned that root 4 is giving off a rootlet. Fig. 18A from the next section shows the roots 3 and 4 in obliquely longitudinal section, the plane of which passes through their central cylinders. The vascular tissue of root 4 can here be traced through the cortex of the stem. The great interest of this series lies in the fact that it shows at one and the same time the characteristic root-structure of these organs and their continuity as endogenous appendages with the stem of *Lyginodendron*.

In order to bring out the point in question more clearly, we have figured one of the roots on a larger scale (Plate 24, fig. 17). This is root 3 of figs. 18 and 18A. The more magnified figure is taken from the third section of the series, in which this root has become free from the stem, and is seen in complete transverse section. The root-like anatomy is here perfectly evident. The primary wood of the central cylinder has seven angles, at which the smallest tracheæ are situated, and is thus of *heptarch* structure. A certain amount of conjunctive parenchyma is present among the primary tracheæ. There is a zone of secondary wood, which is so distributed that a principal ray corresponds in position to each of the protoxylem angles of the primary wood. The inner cortex is somewhat lacunar, and contains a great number of the dark-coloured elements, which we regard as secretory sacs. The cortex is limited on the exterior by a well-marked zone of large, clear elements.

This brings us to our second point. Not only do these appendages of the stem of *Lyginodendron* present all the characters of roots, they are further identical with *Kaloxylon Hookeri*. This becomes evident at once on comparing our fig. 17 with Memoir VII., Plate 5, fig. 23, or with other transverse sections represented in Memoirs VII. and XIII., or again with our own, Plate 20, photograph 13, all of which represent transverse sections of typical *Kaloxylon*. In every respect the identity is perfect: in the structure of the primary wood, the character and arrangement of the secondary tissues, the details of the cortex, and especially in the characteristic external zone, termed the "epidermal layer" in previous memoirs.[*] In all the points, in fact, by which *Kaloxylon Hookeri* was characterized, the roots of *Lyginodendron* show an exact agreement with that fossil.

If, after the consideration of this specially clear case, we refer back to photographs 8, 9, and 10, we shall see that the roots there figured are of the same nature, though their *Kaloxylon* structure is less obvious, owing to slight modifications in that part of the root, which passes through the cortex of the stem.

As regards the distribution of the adventitious roots on the stem, we have little to add to what has already been said. The bases of roots are very commonly found, especially on the larger stems. On the other hand, they were not present on all parts of the stem. Thus the series 1191–1198, which extends through the whole length of an internode, with the adjacent nodes, nowhere shows any sign of an adventitious root.

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[*] Williamson, "Organization," Part VII., 1875, p. 16; Part XIII., 1887, p. 295.

The roots occur on all sides of the stem, a point of some importance with reference to the habit of the plant. Longitudinal sections show that they were scattered quite irregularly, occurring both on nodes and internodes; their position shows no relation to that of the leaves.* We arrive, then, at the following conclusions:—

1. The stem of *Lyginodendron* bore numerous adventitious roots of endogenous origin, which occurred both at the nodes, and on the internodes.

2. These adventitious roots are identical with the fossils previously described under the name of *Kaloxylon Hookeri.*

2. *Primary Structure of the Root.*

The organization of *Kaloxylon Hookeri* has been fully described and illustrated in former memoirs.† Now, however, that its true nature is known, it becomes necessary to reconsider its structure in the light of our present knowledge.

When once the right clue has been obtained, there is no difficulty in recognizing all the specimens of *Kaloxylon* as roots. This is evident on inspecting the various figures in Memoirs VII. and XIII., or our own photographs 11–15. Following our usual course, we will first consider the primary structure of the root, and then the changes due to cambial activity.

The central cylinder of the root, before the commencement of secondary thickening has a perfectly typical radial structure, the number of xylem-groups varying from 8 down to 3, or possibly even 2 in the finest rootlets. The smallest primary tracheides are invariably at the peripheral ends of the radiating xylem-strands (see Plate 20, photograph 11 and Plate 25, fig. 20). That these peripheral elements really represent the protoxylem is proved by radial longitudinal sections, such as that shown in fig. 19. This section passes exactly through one of the primary strands of wood, and shows a narrow spiral tracheide, *px*, at its outer limit. Towards the interior the tracheides become rapidly wider, and here their walls are pitted. The border of the pits is sometimes well preserved. The absolute dimensions of the more central tracheides vary greatly, the diameter ranging from ·0[illegible] to ·09 millim. in different specimens.

Among the tracheides there is a considerable amount of conjunctive parenchyma, which is relatively most abundant in the largest steles. Sometimes this tissue separates the xylem-groups from one another (see photograph 11), sometimes it is irregularly scattered among the tracheides (see photograph 12). The conjunctive parenchyma consists of square-ended prismatic cells (see fig. 19). This combination of tracheides and parenchyma gives a highly characteristic appearance to the transverse sections of the larger steles. The parenchymatous bands sometimes extend to the centre of the cylinder, but we never find a definite pith. Secretory sacs sometimes occur in the conjunctive tissue.

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* The most important preparations for the connection between root and stem are the following:—C.N. 1144, A.; 1144, B.; 1147; 1148; 1883; 1885; 1885, A., B., and C. (same specimen); 1885, I., K., and L. (same specimen); and 1981.

† Williamson, "Organization," Parts VII. and XIII.

The best transverse sections of young roots show the primary phloëm-groups quite clearly (see photograph 11 and fig. 20, *ph.*). They are distinguished at once from the conjunctive parenchyma by their smaller cells, with thinner walls, and by a peculiar brownish tint, which may be due to the presence of carbonaceous matter derived from the abundant cell-contents. These groups alternate in a perfectly regular way with the xylem groups (photograph 11, fig. 20). They are always separated from the adjacent xylem by one or more layers of conjunctive parenchyma. In longitudinal sections, the elongated phloëm elements are even more sharply distinguished from the short-celled parenchymatous tissue (C.N. 1633).

The limits of the central cylinder are not very well defined. It appears, however, that the pericycle was one cell only in thickness, at least, opposite the xylem-groups, though sometimes thicker opposite the phloëm, and that the layer next beyond this, which has rather stouter walls, represents the endodermis (figs. 19 and 20). It is only in the rarest cases that any trace of the radial marks* characteristic of endodermal cells can be distinguished.

The broad inner zone of the cortex, constituting the greater part of its bulk, consisted of lax somewhat lacunar parenchyma, traversed by an enormous number of secretory sacs, the dark contents of which give a characteristic appearance to the sections (see photographs 11–14, figs. 17, 19, and 20). The transverse septa in these sacs are very evident in longitudinal sections, proving that these organs were formed from cells and not from intercellular canals.

In this cortical zone branched and septate fungal hyphæ are often met with—a proof, if any were needed, that true Fungi ("Mycomycetes" of BREFELD) already existed in the Carboniferous epoch.

The outer zone of the root is formed by the very well-marked "epidermal layer," consisting of two or more series of rather large thin-walled cells, which are often much better preserved than the rest of the cortex, so as to stand out conspicuously, when the more internal tissue has become disorganized (see the various figures in Memoirs VII. and XIII., also Plate 24, fig. 17 of the present paper). The general appearance of this layer is often suggestive of a velamen, but there are no special markings on the cell-walls. We find no signs, even in the youngest rootlets, of any cells exterior to this zone, which we may therefore assume to have been really superficial. No root-hairs have been observed, but the external cells are often somewhat papillate. We may speak of this zone as the *outer cortex* or *epidermal layer* indifferently, for we have no means of determining its strict morphological nature.

The typical roots of *Lyginodendron* usually attain, before secondary thickening, a diameter of from 2 to 2½ millims. The largest root has a diameter of 7 millims. This possesses a considerable zone of secondary tissue, but even without this the diameter would have been about 5 millims. We also find, however, many rootlets of quite small dimensions, several examples of which were figured in Memoir XIII. It requires a good deal of care, in the case of these very minute specimens, to determine with certainty to what plant they belong. We believe, however, that the structure of the cortex may be safely relied on. Where the inner cortex consists of lax tissue, with very numerous secretory sacs, while, at the same time, the well-marked "epidermal layer" is present, we feel justified in referring the rootlet to *Lyginodendron*. The organs with which confusion is possible are :

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* They are visible in a small tetrarch root (C.N. 1234), previously figured on a small scale, WILLIAMSON, "Organization," Part XIII., Plate 24, fig. 22.

1. The finest rootlets of *Calamites,* formerly known as *Astromyelon* ;* and
2. Those of *Rhizonium,* a root of unknown affinity.

From the Calamitean rootlets, those of *Lyginodendron* can usually be distinguished by the absence of the thick-walled superficial layer, which is so characteristic of the former. The inner cortex of the rootlets of *Lyginodendron* has also less definite lacunæ than that of the rootlets of *Calamites,* a distinction which, however, becomes of doubtful value in the case of the very finest rootlets.

The rootlets of *Rhizonium* differ from those of *Lyginodendron* in the entire structure of the cortex, which is formed throughout of uniform closely-fitting cells, with few secretory sacs. *Rhizonium* † is also characterized by its extraordinarily abundant branching, much exceeding that even of the roots of *Lyginodendron.* In some even of the small rootlets, the identification is quite satisfactory. Thus *triarch* rootlets, with the characteristic structure of the *Lyginodendron* root, are found, as to the true nature of which there can be no doubt.‡

When Memoir XIII. was published, the fact that these finer branches were rootlets was already recognized as probable, though *Kaloxylon* was at that time regarded as an independent plant. The doubt suggested in that memoir as to the centripetal development of the xylem disappears as soon as we realize that the rootlets of different sizes are not developmental stages of the same organ, but represent branches of different orders or simply of different dimensions.

The typical roots of *Lyginodendron,* before the commencement of secondary growth, often bear a striking resemblance to the smaller roots of recent Marattiaceæ. On the other hand, they have little in common with those of any Cycadeæ at present investigated.

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* See "Further Observations," &c., Part II. The Roots of *Calamites.*

† See Williamson, "Organization," Part XV., Plates 3 and 4, figs. 16–21.

‡ As in C.N. 1907, where triarch rootlets of *Lyginodendron* and of *Rhizonium* lie side by side. The former measures about ·6 millim. in diameter. The still smaller rootlets, some of which are diarch, are more doubtful, but some of them, such as those figured in Memoir XIII., most probably belong to our plant.

3. *Secondary Tissues of the Root.*

Among the numerous specimens of roots of *Lyginodendron* which we have examined, we find the secondary tissues in every stage of development, from their first appearance (see Plate 20, photograph 12 and Plate 25, fig. 20) up to a stage when the secondary wood has attained a radial thickness of about 20 cells (see photograph 14). The process takes place exactly in the manner typical for roots of Dicotyledons, so that this fossil might very well be used for purposes of demonstration as illustrating the secondary growth of a root with diagrammatic clearness.

The cambium first appeared immediately within the groups of phloëm, arising from the division of the conjunctive cells lying in that position. It thus formed at first a series of isolated arcs separated from one another by the protoxylem-groups. This is well seen in fig. 20 which shows the first layer of wood formed from the cambium, *cb.*[*] It is probable, that in the meantime a few additional tracheæ, the "metaxylem" of VAN TIEGHEM (*loc. cit.*, p. 684), had been differentiated from the conjunctive tissue between the primary groups of xylem (*cf.* photograph 11 with photograph 12).

The cambial divisions soon spread to the pericycle outside the protoxylem-elements (see photograph 12) so as now to form a complete though not a circular ring. The whole ring, however, did not behave alike. Opposite the primary phloëm, secondary xylem consisting of tracheæ with narrow secondary rays was formed, while outside the primary xylem, parenchyma, constituting the large principal rays, was at first chiefly developed.[†]

We thus find the secondary tissues broken up into distinct bundles corresponding in number and position to the primary groups of phloëm and separated from one another by the principal rays, which correspond to the protoxylem-strands. In fact, the mode of secondary growth is exactly that which is characteristic of a large number of roots among recent Dicotyledons.[‡] Among Gymnosperms, curiously enough, we find a less close analogy, though in some of the finer roots of Cycads, as, for example, in rootlets of *Stangeria*, the process is essentially similar.

Sooner or later the principal rays often become sub-divided by the intercalation of additional strands of xylem and phloëm (see especially photograph 14).

The details of the secondary wood require no special description. It is composed of tracheides and rays exactly as in the stem. The pits of the tracheides are usually limited to the radial walls.[§]

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[*] See also WILLIAMSON, "Organization," Part XIII., Plate 24, fig. 27; *cf.* VAN TIEGHEM'S figure of the root of *Pisum*, "Traité de Botanique," second edition, p. 722, fig. 481.

[†] See photographs 13 and 14, also WILLIAMSON, "Organization," Part VII., Plate 5, figs. 23 and 26; Part XIII., Plate 23, fig. 26.

[‡] See DE BARY, "Comparative Anatomy," English edition, p. 474; VAN TIEGHEM, 'Ann. des Sci. Nat., Bot.,' Series V., vol. 13, 1871, p. 274.

[§] WILLIAMSON, "Organization," Part VII., Plate 4, fig. 29; Plate 5, fig. 27; Plate VI., fig. 30.

Both cambium and secondary phloëm are often preserved in great perfection (see photographs 13 and 14, also WILLIAMSON, Part VII., Plate 6, fig. 31). The phloëm is essentially similar to that in the stem. The position of the primary phloëm groups can still be clearly recognized even in advanced roots (see photographs 13 and 14, also WILLIAMSON, Part XIII., Plate 23, fig. 21).

We find no distinct formation of periderm in the older roots, though sometimes a few tangential divisions took place in the pericycle (see photograph 14). The primary cortex became a good deal compressed by the secondary growth within it, but, so far as our specimens show, it was not thrown off.

Small rootlets, as well as the larger roots, were evidently capable of considerable secondary growth. Thus, the most advanced specimen figured (photograph 14) can have had only a small tetrarch cylinder to start with, and must in its primary condition have been considerably smaller than the other roots figured.

4. *Branching of the Root.*

Specimens showing branches in connection with the principal axis have been previously figured.* Additional specimens are represented in our photographs 10, 12, and 15. The ramification was evidently abundant. Thus, the specimen shown in photograph 12 was giving off four branches, almost at the same level, two of which are shown in approximately median section. The branches were always of considerably smaller size than the main axis. They were evidently rootlets, borne on a relatively main root. Two points of interest arise in connection with these rootlets :—

1. Each rootlet is invariably placed exactly opposite one of the protoxylem-groups of the main root which bears it (see photograph 12, fig. 20, and the figures above cited). This fact is shown with special beauty in the longitudinal section represented in photograph 15. Here one of the rootlets is cut exactly in the median plane, and its connection with the smallest peripheral xylem-elements of the main root is clear. The tracheides of the rootlet bend at a right angle on joining those of the main root. The bend was no doubt directed towards the organic base of the latter.

2. The rootlets are evidently of endogenous origin. Although we cannot observe their development, this is sufficiently proved by the fact that the rootlet always has a cortex of its own, which can be traced through that of the parent root (see photographs 12 and 15, also WILLIAMSON, Part XIII., Plate 24, fig. 27).

In every respect, then, the branching of these organs is that characteristic of roots.

The knowledge which we have now obtained of the roots of *Lyginodendron* forms a striking addition to the characteristics of this extraordinary fossil. We have already pointed out the remarkable combination of fern-like and Cycadean characters presented by the stem and foliage of the plant. We now see that its roots show still more striking peculiarities. With a primary structure like that of the roots of Marattiaceæ they combine a mode of secondary growth which recalls that of a typical *Dicotyledon,* a resemblance which, we need hardly say, is not indicative of affinity.

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* WILLIAMSON, "Organization," Part VII., Plate 6, fig. 33; Plate 7, fig. 34; Part XIII., Plate 24, fig. 27.

D.—Habit and Dimensions of the Plant.

The specimens of *Lyginodendron,* on which the preceding description has been based, are all of comparatively small size, the maximum diameter of the stem not exceeding about 4 centims.

It has been supposed that the plant attained arborescent dimensions. The evidence from this belief is derived partly from certain cortical impressions of large size, partly from a single large specimen, with the structure of the secondary wood preserved, the real nature of which, however, is not certain.

Four examples of the cortical impressions in question were figured in Memoir IV., Plate 27. They obviously represent the casts of a "*Dictyoxylon*" cortex of a very large stem. The furrows, no doubt, correspond to the print of the sclerenchymatous network, the elevations to the soft parenchyma by which the meshes were filled.

A general resemblance to the outer cortex of *Lyginodendron* is obvious; but this seems to be the only reason for connecting these impressions with our plant. The meshes of the cast are of very large size, reaching a length of as much as 8 centims. We have received, through the kindness of Mr. A. C. Seward, F.G.S., a photograph of a still finer specimen of this kind from the "Third Grits" in the neighbourhood of Harrogate. This impression is almost a metre (38 inches) long and 28 centims. ($11\frac{1}{4}$ inches) in maximum width. The meshes of the cast are long and pointed in form and very variable in size, reaching a length of at least 14 centims. Some of the larger meshes are sub-divided by oblique furrows, which no doubt represent the prints of subsidiary connecting strands of sclerenchyma. The specimen seems to be nearly flat, so that it is impossible to form any definite idea of the size of the stem to which it belonged, but it must certainly have been a good-sized tree.

We do not think, at present, that there is any sufficient proof that these large cortical impressions belong to *Lyginodendron.* We have no undoubted *Lyginodendron* in which the meshes of the outer cortex at all approach the dimensions of those in the casts. The length of the meshes in *Lyginodendron* rarely exceeds 6 millims.

It seems quite possible that the large casts may represent the outer bark of some species of *Sigillaria,* in which case their dimensions would present no difficulty. We know that the outer secondary cortex of *Sigillaria* possessed "*Dictyoxylon*" structure,* as is well shown in sections of *Sigillaria spinulosa* from M. Renault's collection.* The meshes in this specimen are sometimes sub-divided by fine sclerenchymatous strands exactly as we find in the casts. The only "Dictyoxylon" cortex, with which we are acquainted in *Lyginodendron*, was primary. We have good evidence that periderm was formed to the interior of this zone, and therefore it seems certain that, if the stem attained any large size, the characteristic cortical layer must have been cast off, and so could not have left the impressions which we see on the casts. We think, therefore, that no convincing evidence for the arborescent dimensions of *Lyginodendron Oldhamium* can be derived from the cortical impressions.

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* See Solms-Laubach, "Fossil Botany," p. 247, &c.

There remains the large specimen showing structure, received from Mr. NEILD, and referred to in Memoir IV., p. 386. The specimen includes the pith and a portion of the wide zone of secondary wood. Sections in the three directions have been cut and clearly exhibit the structure so far as it is preserved.† The diameter of the pith is 3·3 × 2·3 centims. The maximum radial thickness of the secondary wood is 5·8 centims., but we cannot be certain that its whole thickness is preserved. Assuming, however, that we have the whole thickness of the wood, the radius of the stem up to the cambium would have been over 7 centims., and its diameter over 14 centims. We cannot tell what was the diameter of the whole stem, for we know nothing of the cortex. No authentic specimen of *Lyginodendron* which we have seen, however, has secondary wood of a greater thickness than about 6 millims.; so, if we judge by this dimension, the stem in question must have been nearly ten times as large as that of any undoubted *Lyginodendron* in the WILLIAMSON collection.

Unfortunately, the only structure preserved is that of the secondary wood. Its general anatomy is identical with that of certain specimens of *Lyginodendron*.‡ The tracheides are smaller than is usual in *Lyginodendron*, but not smaller than in some undoubted stems of that plant. The radial section shows the muriform rays and the pits on the walls of the tracheides, which, in so far as their preservation allows of comparison, agree very well with those of our plant. The pith is completely disorganized and no trace of the primary wood can be recognized. There is, however, a narrow incomplete zone of internal secondary wood, distinct from the rest, at the margin of the pith—which recalls the anomalous medullary tissue sometimes found in *Lyginodendron*. Although the parenchyma of the pith has perished, the cavity contains clusters of dark brown cells, which are much like the sclerotic nests characteristic of the pith in *Lyginodendron*.

On the whole, until some other fossil has been found which agrees better with this doubtful stem, we think there is a presumption that it really belonged to a *Lyginodendron*, or to some plant of the same type of structure.

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* C.N. 665 and 668 (presented by M. RENAULT). See also C.N. 703, figured in WILLIAMSON, "Organization," Part IX., Plate 25, figs. 93–95.

† The sections are C.N. 1131, 1132, and 1133.

‡ *Cf.* especially C.N. 1124, 1176, and 1183.

Mr. Neild's specimen thus affords a certain amount of evidence that *Lyginodendron Oldhamium*, or some allied species, may have attained the dimensions of a small tree.

As regards the habit of the ordinary small specimens, with which we are familiar, the radial symmetry of the stem and the fact that adventitious roots, when present, are given off on all sides, render it probable that the plant grew in an upright position. The longest piece of stem which we have is barely three inches (7·6 centims.) in length (C.N. 1207 A). The position of the nodes in this specimen is not very evident; two, however, can be distinguished and they are about one inch (2·5 centims.) apart.

From the course of the vascular bundles we know that the total length of the stem must have included many internodes, for, if our interpretation of the facts be correct, it follows that each transverse section of the stem usually shows the traces of the next ten leaves above. We must, therefore, picture *Lyginodendron* to ourselves as having a tall, upright stem rising to a height of several feet and bearing somewhat remote, spirally arranged, highly compound, fern-like leaves. The base of the stem, where the adventitious roots were given off, must have been buried for some depth in the earth or mud. Probably the bases of stems would be the parts most often preserved, which would explain the frequency with which adventitious roots are met with in connection with the stem. It is not probable that the roots were aërial; the fact that they branched freely immediately on leaving the stem militates against such an idea (see photograph 10, fig. 18). The velamen-like outer layer, which might suggest an aërial root, is common to the finest rootlets, and these must almost certainly have been subterranean. The well-developed xylem of the roots renders it probable that they vegetated in a fairly firm soil.

The stem is mechanically well-constructed and thus fitted to maintain an upright position while bearing abundant foliage. We have no distinct evidence for any rhizome-like organs, but it is possible that some of the small shoots which are rather deficient in sclerenchyma may have been creeping or subterranean. The small specimens, which constitute almost the whole of our material, could not have been branches borne on main stems, for in that case they would not have borne adventitious roots. If the plant really attained a relatively large size, then we must assume that our material is made up of *young* specimens.

This brings us to the most important of all questions, that as to the fructification. It is a remarkable fact, that though *Lyginodendron Oldhamium* is one of the commonest of our English coal-fossils, and though all its vegetative organs are preserved with astonishing perfection, no certain traces of reproductive organs have ever been discovered.

If the plants constituting our material had borne anything at all of the nature of a cone, it is difficult to understand why its remains should never have been found. The only cone-like body discovered had, as we have shown above, nothing to do with the fructification.

On the other hand, Fern sporangia are occasionally found among the fragments of *Lyginodendron* foliage, though never in actual continuity with it.*

Two possibilities suggest themselves :

1. It may be, that *Lyginodendron* was, as to its fructification, a true Fern (in spite of its anatomical peculiarities) and bore sporangia on its leaves ; they might very easily have become detached, and the want of any evidence of continuity between sporangia and leaf would not be surprising.

2. It is possible that our material consists entirely of young plants, in which case the absence of fructification is easily accounted for.

On the whole, we incline to the latter view ; if our specimens had often been fructifying ones, it is probable that sporangia, even though detached, would be much more commonly found than is actually the case. The few examples observed are easily explained by accidental admixture of foreign material.

We think, therefore, that the whole question of fructification must be left open for the present.

We shall not enter further into the consideration of affinities, until the genus *Heterangium* has been dealt with, for the two genera throw much light on each other and must be discussed together.

II.—HETERANGIUM, *Corda.*

INTRODUCTION.

The genus *Heterangium* was founded by CORDA in 1845, on a fragmentary specimen from the Bohemian coal-measures. The first British specimens were discovered in 1871 among Mr. GRIEVE's Burntisland fossils. This form was originally named *Dictyoxylon Grievii*, but in 1872 was placed in CORDA's genus, and now bears the name of *Heterangium Grievii*, WILL.†

In addition to the Burntisland specimens, fossils which appear to be referable to the same species were discovered at a later date by Mr. LOMAX, at Dulesgate, in Lancashire.‡

In the mean time, a second species, in a marvellous state of preservation, had been discovered in the Halifax coal-measures. To this form the name of *Heterangium tiliæoides*, WILL., was given.§

A French species, *Heterangium Duchartrei*, B.R., originally referred to the genus *Poroxylon*, was discovered by M. RENAULT, and shows a considerable resemblance to our *H. tiliœoides.* A second species, *H. Bibractense*, B.R., has since been described by M. Renault.[*]

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* See, for example, C.N. 1630, 1979, 1980.

† WILLIAMSON, 'British Association Reports,' 1871 ; "Organization," Part IV., 1872, pp. 394 and 404.

‡ WILLIAMSON, "Organization," Part XVII., 1890, p. 96.

§ WILLIAMSON, "Organization," Part XIII., 1887.

Our present detailed knowledge of the structure of *Heterangium* has been derived almost entirely from the study of the English and Scotch specimens.

As is well known, the genus *Heterangium*, while closely resembling *Lyginodendron* in habit and many points of structure, is sharply distinguished from it by the primary structure of the central cylinder in the stem. In *Heterangium* there is no pith; the whole interior of the stele is occupied by the primary wood, consisting of a mass of tracheæ, arranged in groups and interspersed with irregular bands of conjunctive parenchyma.[†]

Important as this difference is, we find that the agreement in details of structure with *Lyginodendron* is in many points so exact, as to leave no doubt of the close affinity of the two genera. The foliage, of which we have some knowledge in the case of *H. Grievii*, bore a general resemblance to that of *Lyginodendron*. We have good reason to believe that the roots were also of the same type of structure as in that genus.

We will begin our description with *H. Grievii*, the species of which we have the most complete knowledge, though its detailed preservation is seldom equal to that of *H. tiliœoides*.

i. HETERANGIUM GRIEVII, *Will.*

A. THE STEM.

1. *General Structure.*

The stems of *Heterangium Grievii*, so far as our specimens show, rarely exceeded a diameter of 1·5 centim. The smallest stems observed attained about half this diameter (see branch in Plate 26, fig. 21); so the range of dimensions is inconsiderable, contrasted with that among the authentic specimens of *Lyginodendron*. The general structure is uniform throughout, the differences depending almost entirely on the extent to which secondary growth has taken place.

There are some slight differences between the Burntisland and the Dulesgate specimens, though we have not regarded them as sufficient to necessitate a specific separation between these forms.

The typical structure has been so fully described in former memoirs, that only a brief recapitulation is necessary here.[‡]

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[*] Renault, "Structure comparée de quelques tiges de la Flore carbonifère," 1879, pp. 276–278, Plate 14, figs. 4–8. Bertrand and Renault, "Recherches sur les *Poroxylons*," 'Archives bot. du Nord de la France,' 1886, p. 245. Renault, "Flore fossile d'Autun, &c.," Part II., Atlas, Plate 65, 1894.

[†] See Williamson, "Organization," Part IV., Plate 28, fig. 30; Part XIII., Plate 21, fig. 1; Plate 22, fig. 2; also our Plate 28, fig. 30.

[‡] Williamson, "Organization," Parts IV. and XVII.

The central cylinder, with its large axial mass of primary wood, traversed in all directions by anastomosing bands of parenchyma, by which the tracheæ are separated into irregular groups, presents a most characteristic appearance. We recognize at once that the smaller elements of the primary wood lie near the periphery, where we can distinguish definite groups of tracheæ, recalling the perimedullary xylem-strands of *Lyginodendron* (see Plate 26, figs. 21 and 24 ; also WILLIAMSON, Part IV., Plate 28, fig. 30 ; Part XVII., Plate 14, fig. 14). The whole structure at first suggests a Lycopodiaceous stem a suggestion which, as we shall see, is altogether fallacious. A better parallel will be found in certain stems of Ferns.

In many stems the primary structure has remained unaltered (fig. 21 ; WILLIAMSON, "Organization," Part XVII., Plate 14, fig. 14) ; in others a certain amount of secondary wood has been added. At the exterior of the secondary wood the cambium and phloëm are found in favourable cases (see fig. 24), though not so well preserved as in *Lyginodendron* or in the next species of *Heterangium*.

The cylinder is surrounded by a zone of rather large clear cells, very well marked in many cases, which we regard as constituting a pericycle (see Plates 26 and 27, figs. 21, 26, 28, *pc.* ; WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30, *g.*). The inner cortex is of great width, and consists of parenchyma, in which are imbedded large and conspicuous nests of sclerotic tissue (fig. 21, *sc.*). In longitudinal section we see that these nests form horizontal bands—a most characteristic feature of both stem and petiole (figs. 22, 23, 28 ; WILLIAMSON, "Organization," Part IV., Plate 29, fig. 32 ; Plate 31, figs. 45 and 47 ; Part XVII., Plate 15, figs. 17 and 18).

The outer cortex is of the "*Dictyoxylon*" type, but with narrower parenchymatous meshes than in *Lyginodendron* (WILLIAMSON, Part IV., Plate 28, fig. 30 ; Plate 29, fig. 35). In young specimens the parenchymatous bands are very inconspicuous (fig. 21). Leaf-trace bundles are scattered throughout the inner cortex, and can readily be traced from the pericycle out into the bases of the leaves (see WILLIAMSON, "Organization," Part IV., Plate 30).

The outer surface of the stem was distinctly ribbed, the ribs, no doubt, corresponding to the decurrent bases of petioles. The "restoration" of a portion of the stem, represented in WILLIAMSON, "Organization," Part IV., Plate 31, fig. 49, still appears to us, after our renewed investigations, to be accurate in all essential points.

Apart from the structure of the stele, the chief differences from *Lyginodendron* which strike us in a general survey of the organization of the stem are in the distribution of the sclerotic nests and in the course of the vascular bundles.

In *Heterangium*, the former distinctly belong to the cortex, while in *Lyginodendron* they are usually limited to the pericycle. The vascular bundles in *Heterangium* leave the pericycle early in their outward course and pass gradually outwards through the cortex, while in *Lyginodendron* they keep within the pericycle until they approach their exit from the stem.

2. *Course of the Vascular Bundles.*

The main facts as to the course of the vascular bundles in *Heterangium Grievii* have always been understood, since the first description of the plant was published in 1872. A series of eight transverse sections from a piece of stem nearly two inches long, figured in Part IV., Plate 30, affords conclusive proof that the vascular bundles, which are found in the cortex, pass gradually outwards and enter the bases of the leaves, each of which receives a single bundle. At the same time the lower ends of these bundles were traced downwards to their point of union with the central cylinder.*

It has only been necessary for us to consider two points :—

1. What light does the course of the bundles throw on the phyllotaxis of the plant ?

2. To what extent can the leaf-trace bundles be recognized, as distinct strands, at the periphery of the primary wood ?

Some of the specimens are sufficiently complete and well-preserved to enable us to determine the succession of the leaf-trace bundles in the same way as was done for *Lyginodendron* (p. 708).

In some of the larger stems as many as nine or even ten leaf-traces are seen in the transverse section, counting all those which have once begun to separate from the central cylinder. Their arrangement points distinctly to a $\frac{3}{8}$ divergence.† In one case, for example, the 9th bundle (counting from within outwards) lies directly outside the 1st, while the 10th corresponds in like manner to the 2nd. Here the phyllotaxis must evidently have been $\frac{3}{8}$. It is possible that a higher divergence may have sometimes occurred. In the smaller stems a $\frac{2}{5}$ arrangement has been observed (C.N. 1293).

As regards the second question, the careful observation of good transverse sections shows clearly that the arrangement of the tracheæ in the primary wood is not an irregular one, but that a number of definite bundles can be distinguished at the periphery of the stele. These peripheral strands have essentially the same structure as the xylem of the leaf-trace bundles, with which they are in continuity.‡

We have now determined that each of the peripheral groups corresponds very exactly in structure with one of the perimedullary strands of xylem of *Lyginodendron.* In *Heterangium* the number of these strands at the periphery of the cylinder is very large—(from 16 to 20)—greatly in excess of the number of orthostichies which appear to have existed. This is a point of difference from *Lyginodendron,* in which, as we have seen, the number of perimedullary strands is either equal to that of the cortical leaf-traces or not greatly in excess of it.

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* WILLIAMSON, "Organization," Part IV., p. 401 ; Plate 28, fig. 30, m''', &c.

† The position of the two leaves of which the bases are shown in the series figured in WILLIAMSON, "Organization," Part IV., Plate 30, also indicates a $\frac{3}{8}$ phyllotaxis.

‡ See figs. 21, 24, and 26 ; also the transverse sections figured in "Organization," Part IV.

This we can explain in three ways:

1. The leaf-traces on joining the cylinder may have branched, or
2. They may have extended down through a very large number of internodes turning aside sufficiently to make room for each other, or
3. It may be that some of the peripheral strands of the cylinder are cauline and not directly continuous with the leaf-trace bundles. It is not possible to decide between these suppositions; the strands in question are not isolated like those of *Lyginodendron*, but form part of a continuous mass of wood. Hence their course could only be determined with certainty by tracing the actual protoxylem-elements through a series of sections, and that is more than we can expect to do, though in individual cases the protoxylem is clear enough.

We must, therefore, be content to sum up our knowledge of the course of the bundles in *Heterangium Grievii*, as follows:—

1. The leaves were spirally arranged, the phyllotaxis being $\frac{3}{8}$ in some of the larger, and $\frac{2}{5}$ in some of the smaller stems.
2. Each leaf received a single trace. The traces passed very gradually through the cortex, and joined the central cylinder at a distance below the node equal to from 6 to 10 internodes.
3. The traces can be followed for some distance downwards at the periphery of the central cylinder.

3. *The Primary Structure of the Stele and Leaf-trace Bundles.*

In most specimens the tracheæ occupy the larger part of the whole area of the transverse section of the primary wood.* In some cases the stele is more parenchymatous and the scattered tracheæ form a relatively small part of the whole tissue.† In no case, however, is there any sign of a definite central medulla. The parenchymatous bands extend to the periphery of the primary wood, where they separate the more external xylem-strands from one another, and are continuous with the principal rays of the secondary wood (see fig. 24, *c.p.*).

The conjunctive parenchyma is made up of short, thin-walled, square-ended cells (see fig. 25, *c.p.*).

In the specimens of *H. Grievii* from Burntisland we found no other elements in this tissue; in the stems from Dulesgate, Lancashire,‡ however, the conjunctive parenchyma is traversed by rows of elongated cells with dense carbonaceous contents, similar to the structures which we have termed "secretory sacs" in *Lyginodendron*.

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* WILLIAMSON, Part IV., Plate 28, fig. 30.

† C.N. 1254.

‡ WILLIAMSON, "Organization," Part XVII., p. 96.

There is every reason to believe that the tracheal elements of the primary wood were all *tracheides* and not true vessels. No signs of transverse walls are ever observed, while sometimes we find the very tapering ends of the elements. Their length must have been great, as terminations are by no means frequently seen.

The tracheæ of the interior of the wood are always pitted. Where they are in contact with one another the pits, which are very numerous and hexagonal in outline, are most distinctly bordered, as shown in fig. 25. The borders of the pits, which have not been described before, can only be seen in well-preserved specimens; in many cases the borders have perished, leaving behind an apparently reticulate sculpturing. On the other hand really simple pits occurred on the surface of contact between tracheæ and parenchyma.

The most important point, however, connected with the primary wood is the structure of its peripheral region, for it is here that a clear analogy with *Lyginodendron* shows itself.

The "coalesced clusters of small vessels which occupy the peripheral portion of the vasculo-cellular medullary axis" were described in the first memoir on *Heterangium*, and their continuity with the leaf-trace bundles was also observed.*

We have paid special attention to the structure of these peripheral "clusters" of tracheæ, which in many of the specimens are very distinct. A good typical example is shown, in transverse section, in Plate 26, fig. 24. The close resemblance to a perimedullary xylem-strand of *Lyginodendron* becomes evident if the figure cited be compared with Plate 21, fig. 2. In *Heterangium*, as in the former genus, the smallest elements of the xylem-strand are situated in its interior, though at no great distance from its peripheral surface. In both genera these elements are accompanied by parenchymatous cells. Indications of the spiral thickening of the smallest tracheides can sometimes be observed even in the transverse sections (see fig. 24, *px.*). To determine their true nature, however, recourse must be had to the corresponding radial sections, such as the section represented in fig. 25, which should be compared with Plate 22, fig. 4, from *Lyginodendron*. Here we see that the smallest tracheides have a loosely spiral thickening and evidently constitute the *protoxylem* of the strand.

The elements to the exterior of the protoxylem (x'.), which form the centrifugal part of the primary wood, are more densely spiral. In other cases they are somewhat reticulate. They are quite distinct from the secondary xylem, which in the part figured is represented by a ray (x^2r.). On the interior of the protoxylem we find some parenchyma and then the large pitted tracheides (x.) of the centripetal wood.

The same structure has been found in all the well-preserved specimens, so that there can be no doubt that the peripheral strands of xylem are "mesarch" in the sense defined above (p. 713), and so far resemble the xylem of the foliar bundles in Cycadeæ. It is quite evident that the protoxylem is not peripheral, and that the centrifugal elements exterior to it still belong to the primary wood.*

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* WILLIAMSON, "Organization," Part IV., p. 401.

These definite xylem-bundles, each with its own protoxylem, do not always occupy the whole periphery of the primary wood. They are often separated from one another by portions of the same irregular tracheal groups which extend throughout the whole interior of the cylinder. For convenience of distinction, we propose to apply VAN TIEGHEM'S term "metaxylem" to these latter groups, reserving the term "primary xylem-strands" for those peripheral bundles which are continuous with the leaf-traces. Usually, however, no sharp limit can be drawn between the two, for, as a rule, the xylem-strand passes over gradually on its inner side into the general metaxylem of the cylinder (see Plate 26, fig. 24, *x.* and *m.x.*).

It may be mentioned, that in the specimens of *H. Grievii* from Lancashire, the protoxylem-elements lie somewhat nearer the external surface of the xylem than in those from Burntisland.

We have no information to give as to the structure of the primary phloëm. Remains of soft tissue in a more or less disorganized condition can always be found between the wood and the pericycle, but the structure of this zone is never preserved in stems without secondary thickening.

The pericycle is sharply marked off from the disorganized phloëm-zone; the latter has a characteristic brown tint, while the pericyclic cells are clear (see Plate 27, fig. 26, *p.c.*). The short-celled pericyclic tissue is often well preserved, though its cell-walls are thin. In the Dulesgate specimens the pericycle is traversed by secretory sacs, which are less evident in the original Burntisland form.

It remains to consider the structure of the leaf-trace bundles on their outward course.

Fig. 26 shows the transverse section of one of these bundles, which is just separating from the stele, but is still enclosed within the pericycle. The position of the protoxylem is not certain, but we believe, from the comparison of many sections, that there are two such groups at the points indicated, *px.* Some of the longitudinal sections pass through out-going leaf-trace bundles, and show clearly the position of the laxly spiral elements in the interior of the xylem strand.†

The collateral structure of the bundle figured in fig. 26 is fairly evident; the thin-walled phloëm is tolerably well preserved and undoubtedly seems to be limited to the outer side of the strand. Unfortunately the preservation in *H. Grievii* is seldom sufficiently good to enable us to decide, with certainty, whether the bundles in the outer part of their course are collateral or concentric. In the original Burntisland specimens a certain amount of tissue has usually perished all round the xylem of the bundles in the cortex, and there is no means of telling whether the whole of this delicate tissue consisted of phloëm. The Dulesgate specimens are somewhat better preserved in this part, so that in some cases it is possible to see that the phloëm of the cortical leaf-traces is limited to the external side of the xylem.*

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* The best slides for showing the protoxylem and primary xylem-strands are :—

Transverse, C.N. 1291, 1293, 1294 (Burntisland).
1915 C. (Dulesgate).
Longitudinal, C.N. 1266, 1268 A, 1276, 1286, 1288 (Burntisland).
1915 G. (Dulesgate).

† The following preparations show leaf-trace bundles in longitudinal section: C.N. 1265, 1282, 1284, and 1915 G.

We may, therefore, regard it as probable that the collateral structure shown in fig. 26 was maintained throughout the course of the bundle in traversing the stem. Although the leaf-trace bundles sometimes became somewhat lobed (as seen in transverse section) in passing through the cortex, yet we have no clear evidence that they ever divided into twin bundles as in *Lyginodendron.*

Our knowledge of the primary structure of the stele and vascular bundles of *H. Grievii* may be summed up as follows:

1. The stele consisted of a central mass of primary xylem (made up of tracheides and conjunctive parenchyma) surrounded by a zone of phloëm. The whole was enclosed by a well-marked pericycle.
2. The primary wood may be divided into the peripheral xylem-strands, which are continuous with the leaf-trace bundles, and the metaxylem. Each of the peripheral strands had the same mesarch structure as the perimedullary strands of *Lyginodendron,* or as the xylem of the foliar bundles in Cycadeæ.
3. The leaf-trace bundles were collateral in structure on leaving the central cylinder and probably remained so in passing through the cortex.
4. The primary tracheides, with the exception of the protoxylem and adjoining elements, possessed numerous bordered pits.

4. *The Secondary Tissues.*

It is not uncommon to find stems of *H. Grievii* which retain the primary structure unaltered, such as the stem represented in Plate 26, fig. 21, where the main axis is quite without any secondary tissues, though, curiously enough, they are present to a small extent in the branch. The majority of the stems, however, have a secondary zone, which is often of very unequal thickness on different sides of the same stem, and is on the whole less developed than in *Lyginodendron.* The secondary wood is very sharply marked off from the primary; this is owing partly to the regular radial arrangement of the secondary elements and partly to their smaller size (see Plate 26, fig. 24; also WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30). In cases where the secondary wood attained any considerable thickness, the size of its elements increased towards the exterior.

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* See especially the four transverse sections C.N. 1915–1915 C.

A local increase in the thickness of the secondary wood is sometimes found near the bases of adventitious roots (see Plate 10, fig. 28, x^2).

The wood has the same structure as in *Lyginodendron*, consisting of radial rows of tracheides, with rays between them (see Plate 26, figs. 24 and 25). The tracheides have numerous bordered pits on their radial walls similar to those of the primary wood. It is probable that a few pits also occurred on the tangential walls, as was certainly the case in *H. tiliæoides*, in which the preservation is more perfect.

The rays consist of thin-walled cells often showing in radial section a characteristic muriform arrangement.*

Fig. 25 shows in radial section the inner part of a ray at a place where the secondary wood is still very thin. The ray is as yet scarcely differentiated from the pericyclic cells by the division of which it arose. Some of the rays are continuous with the conjunctive parenchyma of the primary stele (see fig. 24). We may call these the primary or principal rays, but they do not differ essentially from those which abut on the tracheides of the primary wood. Secondary rays were occasionally intercalated, where the wood attained a sufficient thickness.†

Secretory sacs, which often run in a radial direction, are especially frequent in the rays of the Dulesgate specimens. A figure in a previous memoir gives a sufficient idea of the appearance of the secondary wood as seen in tangential section.‡ The rays, however, are often of greater breadth than those shown in that figure.

Cambium and secondary phloëm are never very perfectly preserved in our specimens of *H. Grievii*, though, as we shall find, their preservation in *H. tiliæoides* is perhaps more perfect than in any other known fossil. In some of the best specimens of *H. Grievii* the tabular form of the cambial cells can be made out in transverse section (see especially Plate 26, fig. 24, *cb.*; also Plate 27, figs. 26 and 29). As regards the phloëm, the transverse sections, as shown in the figures just cited, prove that it consisted of thin-walled elements of smaller diameter than the adjacent cells of the pericycle. Some of the longitudinal sections show that the phloëm-elements were much elongated.§

There is no doubt whatever, that here, as in *Lyginodendron* and in *Heterangium tiliæoides* the cambium was a perfectly normal one, forming wood on its inner and bast on its outer surface.

Where the leaf-trace bundle passes out from the stele a parenchymatous gap is left in the secondary wood, corresponding to the "trace-gap" in *Lyginodendron.*‖

Although we sometimes find traces of tissue-formation by tangential cell-division in the outer layers of the pericycle,* yet the formation of a regular periderm does not seem to have been general in this species.

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* See WILLIAMSON, "Organization," Part IV., Plate 29, fig. 33.

† As in C.N. 1915 C.

‡ WILLIAMSON, "Organization," Part IV., Plate 29, fig. 33*a*.

§ See especially C.N. 1268 A. and 1915 G. and R.

‖ See WILLIAMSON, "Organization," Part IV., Plate 28, fig. 30, m'''.

5. *The Cortex.*

The wide inner cortex consisted of short-celled parenchyma, interrupted by very regular horizontal plates of sclerotic tissue (see Plate 26, figs. 21 and 22†). These sclerotic plates give a most characteristic appearance to the sections both of stems and petioles. They appear to have been of the same nature as the "sclerotic nests," which are so general in *Lyginodendron*, but their distribution is different. In *Lyginodendron* they occurred mainly in the pith and pericycle of the stem and in the cortex of the petioles. In *H. Grievii* they are always cortical in both organs. Their sclerotic character is more easily recognized in the latter plant, where their walls are often prefectly preserved. In some cases, even the numerous fine pits running through the whole thickness of the cell-wall can be distinguished.‡ These elements bear a considerable resemblance to the *stone-cells*, which are so often found in the cortical tissues or petioles of recent plants, as, for example, in *Hoya*.

The sclerotic plates were evidently placed one above the other in vertical series, for a radial section either shows a whole row of them or else misses them altogether.§ The arrangement of their constituent cells is very regular and indicates that they were formed by a special meristem.‖

The outer cortex consisted of the well-known alternating strands of sclerenchymatous fibres and parenchyma. The parenchymatous portions are often very narrow, especially in the Dulesgate specimens, in which the sclerenchyma appears nearly continuous and is only interrupted here and there by small patches of parenchyma¶ (see fig. 21).

The epidermis is sometimes preserved and consisted of rather thick-walled cells. In one case we noticed an appearance suggestive of a depressed stoma, lying over one of the parenchymatous groups of the outer cortex.**

6. *Branching of the Stem.*

We have only a single specimen in which the branching of the stem is shown. This is one of those from Dulesgate. A transverse section of this specimen is shown in Plate 26, fig. 21. The continuity of the cortical tissues of the branch with those of the main axis is evident. Although the branch shows no leaf-traces, it is certainly a stem-structure. It is not a root, for its origin is clearly exogenous. It is not a leaf, for the stele has the same structure as that of the stem, and has even formed some secondary wood. The structure of the cortex of the branch is identical with that of the main stem. We have other sections of the same specimen, one of which shows the branch at a point where it has just become free from the parent axis.*

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* C.N. 1276.

† Also WILLIAMSON, "Organization," Part IV., Plate 29, fig. 32, h', and Part XVII., Plate 15, figs. 17 and 18.

‡ See C.N. 1915 F.

§ C.N. 1276.

‖ WILLIAMSON, "Organization," Part XVII., Plate 15, figs. 17 and 18.

¶ WILLIAMSON, "Organization," Part XVII., Plate 14, fig. 14.

** C.N. 1915 M.

B. The Leaf.

1. *Connection between Leaf and Stem.*

Several specimens show the bases of petioles in connection with the stem. Thus, in the series of sections previously figured the bases of two petioles are shown.† The same series contains a transverse section of another petiole, which has become free from the stem.‡

We have figured in Plate 26, fig. 22, a longitudinal section of a stem, passing through the insertions of two petioles (*pt.*). These examples show that the leaves were inserted alternately on the stem. The length of the internodes shown in fig. 22 appears to have been only about 5 millims. In the series first mentioned the length of the internodes must have been much greater, for the bases of two leaves only were met with in a piece of stem nearly two inches long. Fig. 22 shows that the cortex of the petiole contained the same horizontal sclerotic bands as that of the stem. In most specimens it is evident that only a single bundle entered the leaf from the stem, and not a double bundle, as in *Lyginodendron.* The only exception is one of the Dulesgate specimens, in which two quite distinct bundles are seen in transverse section in the cortex, which appear from their position to be destined for the same petiole.§

In most respects the leaf-traces agree closely with those of *Lyginodendron.*

The specimens showing petioles in connection with the stem enable us to identify other petioles, which have become free. Their cortical structure is quite characteristic, owing to the horizontal sclerotic plates of the inner cortex and the "*Dictyoxylon*" structure of the outer zone. The only difficulty is the possibility of confusion with the petioles of *Lyginodendron.* Two distinctions, however, exist.

1. The characteristic emergences, to which the petioles of *Lyginodendron* owed their former name of *Rachiopteris aspera*, are absent from the petioles of *Heterangium Grievii.*

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* C.N. 1885 H.

† Williamson, "Organization," Part IV., Plate 30, figs. 42 and 44.

‡ C.N. 1244.

§ C.N. 1915 M.

2. The secretory sacs, which are so conspicuous in petioles of *Lyginodendron*, are either absent, or, at least, much less noticeable in those of *Heterangium*.*

2. *Form and Structure of the Leaf.*

We are only able to obtain a very general idea of the form of the leaf in *H. Grievii*. Several of the preparations show a confused mass of petioles of various orders, intermixed with fragments of leaflets. The petioles vary in diameter from 4 millims. to 0·4 millim., or even less. All alike show the characteristic structure of the cortex, which distinguishes these petioles from that of any other known plant, with the exception of *Lyginodendron*, from which they can be separated by the characters mentioned in the last paragraph. In some of the specimens the branching of the petioles is shown. Plate 26, fig. 23, represents a small portion of one of the preparations in question, but gives only an imperfect idea of the complexity of the mass of foliage which it contains. Sections of leaflets are found among the petioles, and are sometimes in connection with their finer branches. The structure of the leaflets is never well preserved, but the form of the sections indicates a decided resemblance to the leaflets of *Lyginodendron*.

Although the evidence available does not admit of our attempting any detailed reconstruction of the form of the *Heterangium* leaf, yet one conclusion of great importance follows with certainty from the facts observed. The leaf of *H. Grievii* must have been a highly compound one, with a much branched rachis, bearing numerous small leaflets. In other words, the foliage of our plant was certainly of a Fern-like character, and was totally different from any leaves known among the Lycopodiaceæ.

Our knowledge of the structure of the leaf is practically limited to that of the petiole and its branches. It is true that in some of the preparations from the Dulesgate specimens beautiful sections of leaflets are shown.† Unfortunately, however, these preparations contain specimens of *Lyginodendron*, as well as of *Heterangium*, so it is impossible to decide for certain to which plant the leaflets belong.

The sections of the petiole are not equal to those of *Lyginodendron*, but the chief points in the structure can be determined. The vascular bundle was no doubt concentric. The central mass of wood is always surrounded by a zone of thin-walled tissue, which, though imperfectly preserved, can hardly be interpreted otherwise than as phloëm.‡

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* For specimens showing leaf-bases in connection with the stem, see the series C.N. 1240–1247; also C.N. 1281, 1286, 1294, 1915 A, and 1915 M.

† See C.N. 1915–1915 C.

‡ Transverse sections of the petiole are contained in the following preparations: C.N. 1244, 1283, 1289, 1300. The last-named is figured in WILLIAMSON, "Organization," Part IV., Plate 28, fig. 46. It was then termed "a young twig." For longitudinal sections see especially C.N. 1286, 1287, and 1292.

The structure of the xylem is essentially similar to that of the petiolar bundle of *Lyginodendron*. The majority of the tracheides are spiral or reticulate, but some are pitted. The lax spiral elements (protoxylem) lie in the interior of the strand.

The structure of the cortex of the petioles has been sufficiently described above.

One point remains to be discussed; in two, at least, of the preparations, sporangia, like those of certain Ferns,* are found in association with *Heterangium* foliage.† A portion of one of these preparations is represented in fig. 23. The sporangium, *sm.*, is in close contact with a fragment of leaf, which appears to be continuous with a small petiole of *Heterangium.* If the continuity between the sporangium and the leaf could be established, the fact would be of the greatest importance. Careful examination of the preparation, however, leads us to doubt much whether this was the case. The fragment is in bad condition, and we found it impossible to prove that the shred of tissue on which the sporangium is seated, really belonged to the *Heterangium* foliage.

The other preparation in question (C.N. 1292) contains numerous sporangia, none of which, however, are connected with the foliage. This slide contains petioles of *Rachiopteris Oldhamia,* WILL., as well as of the *Heterangium,* so that here it is plain that no definite conclusion can be drawn. In other cases *seeds* have been found in association with specimens of *Heterangium,*‡ but there is not the slightest reason for supposing that they have anything to do with our plant. Here, again, the question of fructification must for the present remain undecided.

Our conclusions as to the foliage of *Heterangium Grievii* are the following:—

1. The leaves were arranged spirally on the stem, the phyllotaxis being usually either $\frac{3}{8}$ or $\frac{2}{5}$.
2. The leaves were repeatedly compound, with long and much-branched petioles, bearing small leaflets.
3. The petiole contained a single vascular bundle of concentric structure.
4. The cortex was characterized by the horizontal sclerotic plates in its inner zone and by the "*Dictyoxylon*" structure of its external portion.
5. Both in form and structure, so far as they can be determined, the leaves of *Heterangium* closely resembled those of *Lyginodendron* and were of a Fern-like character.

C. THE ROOT.

1. *Connection between Root and Stem.*

Several specimens of *Heterangium Grievii* show adventitious roots in connection with the stem. Two such specimens have been previously figured, both of which are seen in transverse section of the stem, the root passing out through the cortex in an approximately horizontal direction.*

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* *Cf.* WILLIAMSON, "Organization," Part VIII., Plate 7, fig. 29.

† C.N. 1287 and 1292.

‡ C.N. 1915 D, G, H, and O.

There can be no question that these appendages were really roots. In both cases the organ possesses a cortex of its own, distinct from that of the stem on which it grows. The organs in question must, therefore, have been *endogenous* in origin.

We have figured part of a remarkably fine longitudinal section from one of the Dulesgate specimens, showing the bases of three adventitious roots, placed one above the other in a vertical row (Plate 27, fig. 28). This specimen has the central cylinder, including the pericycle, preserved in great perfection; the cortex, however, is almost destroyed, so that at first there seemed to be some doubt whether the main axis was a root or a stem. That the latter is the case is proved by the persistent cortical sclerotic masses (*sc.*), which are quite characteristic of the stem, and also by the fact that another part of the section shows a leaf-trace bundle, passing through the pericycle.

One of the three adventitious roots is seen in exactly median section. The connection of its tracheæ with those of the primary wood of the stem is quite clear; the root lies exactly opposite one of the protoxylem strands of the stem. The base of the root has formed some secondary wood, which is continuous with that of the parent stem. The phloëm is not shown in this root, but can be recognized in the next, which, as well as the third one, is cut somewhat tangentially. In all the roots the limits of their cortex can be traced. The stem has formed a much larger amount of secondary wood near the bases of the roots than elsewhere. This wood is chiefly developed *above* the insertion of the roots, *i.e.*, in the direction towards the apex of the stem, as determined by the course of the leaf-trace bundles. The pericycle has also undergone an enormous thickening, with tangential cell-divisions, around the bases of the roots. Between their bases secondary tissue, partly consisting of wood, has been formed in the pericycle in a very anomalous manner; much of this tissue is seen in transverse section, so the direction of the tracheides must have been tangential with reference to the stem. There seems, in fact, to have been a special "réseau radicifère," as it is called by VAN TIEGHEM,† in connection with the bases of these roots.

In fig. 29 we have shown a curious structure which we think may probably represent a very young root enclosed within the cortex of the stem. The section is a nearly complete transverse one of a good-sized stem with a considerable amount of secondary wood. The root-like organ is embedded in the cortex, immediately beneath the outer sclerenchymatous layer, and is seen in approximately transverse section.

A central cylinder can be distinguished, but we could detect no lignified elements.

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* WILLIAMSON, "Organization," Part IV., Plate 30, fig. 36; Part XVII., Plate 14, fig. 14.

† "Traité de Botanique," p. 787. The same structure is beautifully shown in transverse section in C.N. 1915 A.

The more central cells of the cylinder are relatively large and may well represent undeveloped tracheæ. Immediately outside the latter we find groups of small cells, possibly young phloëm. The outer layers of the wide cortex are large-celled, as in roots of the "*Kaloxylon*" type. Numerous "secretory sacs" are present throughout the tissues of the organ. We see no other explanation for this structure than that it represents a young adventitious root, and, if so, it is of some interest, for organs at such an early stage of development are necessarily rare in the fossil state. The presence of such a rudimentary root in a mature stem is not very surprising, for we know that adventitious roots may arise at all ages of the stem, and also that such roots may remain for a long time undeveloped.*

2. *Structure of the Root.*

Our knowledge of the structure of the root in *H. Grievii* is at present a matter of inference rather than of absolute proof, for we have no clear transverse sections of those roots which are in actual connection with the stem. The longitudinal sections of the root-bases show that the xylem extended to the centre of the cylinder, and mainly consisted of tracheides like those of the stem.

In the Burntisland preparations transverse sections of roots are rare and unsatisfactory. The Dulesgate specimens, however, contain many beautifully preserved roots, which in some of the preparations are seen in transverse section in close contact with the same stems on which the bases of adventitious roots are found. All these roots are of the "*Kaloxylon*" type, and, as the same material contains stems of *Lyginodendron*, it is quite probable that some of them belong to the latter plant. Yet we feel sure that among these roots those of *Heterangium* are included, for we know that the stems of *Heterangium* in this material produced roots freely, and there are no other root-like organs present which could possibly be referred to them. We believe the explanation to be that the roots of *Heterangium Grievii* were themselves of the "*Kaloxylon*" type, and not always readily distinguishable from those of *Lyginodendron.*

There is one special form of root, however, which we feel pretty strongly convinced belonged to *Heterangium Grievii*. We refer to certain tetrarch roots, such as that shown in transverse section in Plate 27, fig. 27. Roots of exactly this kind are excessively common in the preparations from Dulesgate material containing *Heterangium Grievii*, while we have never found them associated with *Lyginodendron* when *Heterangium* is absent. The characteristics of these roots (which, as the figure shows, are often perfectly preserved) consist in the large tetrarch primary wood, with very prominent angles, and in the almost geometrical regularity with which the tissues are arranged. Roots of *Lyginodendron* with a tetrarch cylinder are, it is true, well known, but in these the primary wood is of small extent and has much less prominent protoxylem angles (*cf.* Plate 20, photograph 14). Another distinction consists in the fact that the primary wood in the roots of *Lyginodendron*, when of comparable extent to that of the roots in question, contains a larger amount of conjunctive parenchyma. The difference in anatomical "habit" between the roots which we are describing and those of *Lyginodendron* is well marked, though easier to see than to describe (*cf.* photographs and figures of *Lyginodendron* roots with fig. 27).

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* The best preparations illustrating the connection between root and stem in *H. Grievii* are C.N. 1260, 1294, 1915, 1915 A, 1915 G, and 1915 H.

The cambium and phloëm are exquisitely preserved in this and other specimens. The secondary thickening took place with remarkable regularity, the bands of secondary wood being strictly limited to the regions opposite the phloëm. The pericycle appears to be several cells thick opposite the protoxylem. The inner cortex, which is a good deal crushed in most of the specimens, contained a large number of "secretory sacs." The large-celled outer cortex or "epidermal layer" is extremely conspicuous.

Longitudinal sections of this form of root show little difference from the root of *Lyginodendron*, except the smaller amount of conjunctive tissue.

From the evidence brought forward we feel no doubt, though the point is not yet strictly demonstrated, that the adventitious roots of *Heterangium Grievii*, like those of *Lyginodendron*, were of the *Kaloxylon* type of structure, but that the special form of root, characterized by a large tetrarch primary stele, with prominent protoxylem angles and little conjunctive tissue, was peculiar to *Heterangium*.*

D. Habit and Dimensions of the Plant.

As regards the dimensions of *H. Grievii* we have no evidence that the stem attained any larger size than is shown in our specimens, which reach a diameter of about 1·5 centim., though, of course, it is quite probable that it may have done so. The habit of the plant must have been like that of a small *Lyginodendron*. The stem was probably upright, as is indicated by its radial symmetry and strong mechanical construction. It bore spirally arranged, highly compound, Fern-like leaves, while in its lower part it gave off adventitious roots. The stem occasionally branched, though apparently this was rare. The general appearance of the plant would probably have been that of a Fern.

As regards the fructification, we have no evidence which we regard as of any weight. We must, however, point out that the entire absence of any cone-like structure is remarkable, especially as in this case there is no reason to suppose that we have to do exclusively with young plants. This negative evidence, if we allow ourselves to be influenced by it at all, rather tends to favour the idea that the plant may have had a Fern-like form of fructification.

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* The best preparations showing this form of root are: C.N. 1885 H, 1915 B, D, M, O, P and R. The "quadrate *Kaloxylon*" shown in C.N. 1635 is probably of the same nature.

ii. HETERANGIUM TILIÆOIDES, *Will.*

This species of *Heterangium* (from the coal-measures of Halifax) was first described in 1887, when a full account of its general structure was given.* The specimens are few, but are remarkable for the astonishing perfection with which the anatomical details are preserved. We are enabled to add some information on the minute structure to the facts previously brought forward.

The stem in its general organization and dimensions resembles that of *H. Grievii.* We do not propose in this case to give a detailed description of the whole structure, which is unnecessary in view of what has already been done, but merely to state in order the fresh points which our renewed examination of the specimens has brought to light.

The first point to which we desire to call attention is the great distinctness of the primary xylem-strands at the periphery of the central mass of wood. They at once strike the observer as definite bundles† (see Plate 28, fig. 32) and can easily be counted. Thus in one of the larger stems‡ they number 20, and in a smaller specimen§ they number 16. The structure of each of these strands is perfectly clear, as shown in transverse section (see figs. 32 and 33), and exactly agrees with that of the corresponding strands in *H. Grievii* or with that of the perimedullary strands of *Lyginodendron* (*cf.* Plate 21, figs. 2, 3, and Plate 26, fig. 24). The spiral or annular protoxylem-elements are placed in the interior of the xylem-strand, but near its outer margin, and are usually accompanied by parenchyma (see the radial section shown in Plate 29, fig. 34). To the outside of the protoxylem we find more densely spiral elements, which evidently still belong to the primary wood, while on the inside tracheides with bordered pits at once appear. It would be quite legitimate to compare the central cylinder of this *Heterangium* to that of a *Lyginodendron,* supposing the primary bundles of the latter to be connected together throughout the pith by a network of metaxylem. The analogy with *Lyginodendron* is more evident in *H. tiliæoides* than in *H. Grievii,* though the structure is essentially similar in these two species. The great majority of the peripheral xylem-strands show the structure described ; a few, however, appear to be destitute of spiral elements.

The secondary growth bore a definite relation to the peripheral strands of the primary wood. Opposite each of the latter a fan-shaped mass of secondary tissue was developed (see fig. 32).‖

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* WILLIAMSON, " Organization," Part XIII.

† WILLIAMSON, " Organization," Part XIII., Plate 21, fig. 1, and Plate 22, fig. 2.

‡ C.N. 1619.

§ C.N. 1620.

‖ Also WILLIAMSON, *loc. cit.*

These masses were separated from one another by the broad principal rays, which were continuous towards the interior with the bands of conjunctive tissue lying between the primary xylem-strands. There was no *inter-fascicular* formation of either wood or bast, and consequently the definite distribution of the secondary tissues gives a very characteristic appearance to the transverse sections.

Both primary and secondary tracheides are nearly though not exactly similar to those of *H. Grievii*; the spirally-arranged bordered pits have narrow inclined slit-like openings.*

The secondary tracheides, in addition to the crowded bordered pits on their radial walls, had more scattered, sometimes simple, pits on their tangential faces.

Many of the secondary rays by which the wood is divided up extend inwards as far as the primary xylem.

In many places the cambium is extremely well-preserved (see Plate 29, figs. 35, 36, and 37). The fascicular cambium is of the usual character, but here, as in *Lyginodendron*, the cambium by which the principal rays were formed shows less frequent tangential divisions.

In the radial section represented in fig. 37, a tracheide (*tr.*) adjoining the cambium is shown, the wall of which is areolated, though not yet pitted in the usual manner. This is evidently a tracheide in course of development; the primordial pits are already marked out, but the deposition of the borders has not yet begun. This is not an isolated case. We have observed in the same material a tracheide, with a still finer areolation, representing a still earlier stage, and another somewhat more advanced, with the borders of the pits beginning to appear. Such stages of histological development are certainly rarities among fossil specimens.

The enormous masses of phloëm constitute the most interesting feature of the fossil. The phloëm attains a thickness little less than that of the secondary wood, and is preserved in marvellous perfection.

The primary rays in passing through the phloëm become greatly dilated, widening out into large wedges, as seen in transverse section, and thus exactly resembling the well-known phloëm-rays of the lime tree, a resemblance to which the fossil owes its specific name.†

At the exterior of each phloëm-strand the irregularly arranged, somewhat thick-walled elements of the *primary* phloëm can be easily recognized (fig. 35, *ph.*). The greater part of the bast, however, is secondary, as shown both by its radial seriation corresponding with that of the cambium and wood, and by the proportion which its thickness always bears to that of the secondary wood.

The secondary rays of the phloëm are often dilated in the same way as the primary rays, but to a less extent. The phloëm groups lying between the rays show no very obvious differentiation of their elements as seen in transverse section (figs. 35 and 36).

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* See WILLIAMSON, Part XIII., Plate 21, fig. 16.

† See WILLIAMSON, Part XIII., Plate 21, figs. 1, 4, and 10; Plate 22, fig. 2; Plate 23, fig. 9.

Longitudinal sections, however, show that the secondary phloëm contained long parenchymatous cells in addition to the sieve-tubes. In the latter transverse walls are not found, and their ends appear to have been tapering (figs. 37 and 38). Generally, the larger elements appear to have been sieve-tubes, but the difference in size is not very marked.

The preservation of the sieve-tubes is astonishingly perfect, so as to leave no doubt as to their nature, a point which was spoken of with some reserve in Memoir XIII. (p. 291), at a time when the detailed structure had not yet been observed. In several cases the sieve-plates on the radial walls of these elements can be recognized with certainty. This is the case, for example, at the place marked *svp.*, in fig. 37, where the markings on the wall clearly indicate a compound sieve-plate. A much better example, however, is shown in the oblique section, from which fig. 38 was drawn. The sieve-tube in question is shown on a larger scale in fig. 38A. The sieve-plates are marked on the wall in brown carbonaceous matter and exactly resemble those of some recent Gymnosperms and vascular Cryptogams. The smallest areas into which the plates are sub-divided no doubt represent the minute sieve-fields within which the actual pores were grouped.

We may well wonder how structures so delicate, which are often difficult to demonstrate in recent plants, can have been preserved in the fossil state. That the markings in question really represent sieve-plates will not be doubted by any botanist who examines the sections for himself and sees how often these appearances occur, and how invariably they are limited to those elements which, from their position and form, must be regarded as sieve-tubes. Sieve-plates in fossil plants have occasionally been figured by previous writers; among the most satisfactory are those shown by Messrs. BERTRAND and RENAULT, in *Poroxylon Edwarsii*, which much resemble those of our plant.*

It is not at all likely that minute differences in the thickness of a cellulose wall, or even minute perforations, would be recognizable so distinctly in the fossil condition. It is much more probable that what we see represents the carbonized remains of that portion of the contents of the tube, which adhered to the plate, so that the sculpturing of the latter has remained in the form of a carbonaceous print.

Beyond the phloëm there is a zone of tissue which we interpret as pericycle; it attained a great thickness, much exceeding that of the corresponding region either in *Heterangium Grievii* or in *Lyginodendron*.† It consisted, like the pericycle of those plants, of short-celled parenchyma, but contained in addition numerous short sclerotic cells either isolated or in groups (see WILLIAMSON, "Organization," Part XIII., Plate 21, fig. 19), a feature in which this species differs from *H. Grievii*, where the sclerotic masses are limited to the cortex, while it agrees with *Lyginodendron.*[*]

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* "Recherches sur les *Poroxylons*," figs. 192 and 193.

† This layer was termed "inner cortex" in Memoir XIII., *loc. cit.*, Plate 21, fig. 1; Plate 22, figs. 2 and 5, *p*.

The outer layers of the pericycle have generally undergone somewhat irregular tangential cell-divisions. Beyond these layers we often find a zone of flattened cells, which may represent an incipient periderm.[†]

Elements of the kind which we regard as secretory sacs are excessively abundant throughout the soft tissues of *H. tiliæoides,* especially in the medullary rays and pericycle.

The cortex, the outer layers of which are usually much shattered, bears a general resemblance to that of *H. Grievii,* especially to the specimens of that type from Dulesgate.[‡]

The leaf-trace bundles are seen in all the transverse sections at various points of their outward course. Sometimes they are met with in the pericycle, sometimes in the cortex. Their close agreement in structure with those of *H. Grievii* or of *Lyginodendron* leaves no doubt as to their nature, though in the present species we have no specimens actually showing their passage into a leaf. One specimen (C.N. 1301) shows a petiole in connection with the stem; the stem is seen in transverse section, the petiole is cut obliquely, but in a nearly longitudinal direction. The continuity of the cortical tissues between petiole and stem is evident. The vascular bundle is well shown in the petiole, but the plane of section does not allow us to trace it into the stem. The structure of the petiole is essentially the same as in *H. Grievii.* It is remarkable that it appears to contain a single vascular bundle only, for the leaf-traces in the stem of this species are nearly always in pairs, as in *Lyginodendron.*[§] The twin bundles may have completely fused on entering the leaf. We think there is no doubt that the pair of bundles imbedded in the pericycle, figured in Memoir XIII., Plate 22, fig. 5, are leaf-trace bundles, which are just separating from the stele, and each of which still retains its own external arc of secondary tissue. Exactly parallel cases are well known in *Lyginodendron* and have been fully described above.

Beyond the fact that the stem bore adventitious roots, we have no information as to these organs. We regard the body represented in Memoir XIII., Plate 23, fig. 12, as the base of an adventitious root at its junction with the wood of the stem. It is very probable that the structure represented in Plate 22, fig. 13, is also connected with the base of a root.

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[*] Some doubt was expressed in Memoir XIII., p. 293, as to these elements being really thick-walled cells. It was suggested that their appearance might be due to the conditions of mineralization producing inorganic deposits on the cell-walls. We now find that the structure of these cells is the same as that of the undoubtedly sclerotic elements which constituted the horizontal plates of the cortex. Like the latter they persist when the surrounding soft tissue has perished. Similar cells occur in the dilated phloëm-rays.

[†] C.N. 1302, 1619, 1627.

[‡] See WILLIAMSON, "Organization," Part XIII., Plate 21, figs. 1 and 6, *r*, *t*; Plate 22, figs. 2 and 11, *r*, *t*.

[§] See WILLIAMSON, "Organization," Part XIII., Plate 22, figs. 7 and 8.

H. tiliæoides appears to us to agree in all essential points of structure with *H. Grievii* and certainly to be rightly placed in the same genus. It differs from that species in the exceptional development of its secondary phloëm and phloëm-rays, in the greater distinctness of the primary bundles at the periphery of the stele, in the consequent separation of the secondary tissues into distinct strands, in the presence of sclerotic elements in the pericycle, and in the double leaf-trace bundles. In several of these points the present species approaches *Lyginodendron* somewhat more nearly than *H. Grievii* does. On the whole, we must regard *H. tiliæoides* as the more highly differentiated of the two *Heterangiums*. Its great interest to the botanist depends chiefly on the extraordinary perfection with which the details of its structure are preserved, affording the clearest proof, that in the carboniferous flora, the histological elements were identical with those of existing plants, however much the arrangement of these elements may have differed.

iii. ON A *Heterangium* OF UNCERTAIN SPECIES.

We have a single specimen of the stem of a *Heterangium*, probably from Halifax, which we are not able to refer with certainty to either of the preceding species. A transverse section of this specimen is shown in fig. 30, and a part of the longitudinal section in fig. 31. The general structure of the stele agrees with that of the other two species. The appearance of the transverse section rather suggests *H. tiliæoides* than *H. Grievii*. The presence of sclerotic groups in the pericycle is a definite character in which it resembles the former species. The longitudinal section, however, shows that the primary tracheides exactly resemble those of *H. Grievii*, while they are somewhat different from those of *H. tiliæoides*. In the latter many of the primary tracheides show curious spiral lines of thickening between the series of pits. Nothing of the kind is visible in *H. Grievii* or in the undetermined specimen. Only a very slight formation of secondary wood has taken place in this specimen. The cortex is of moderate thickness and has a smooth outer surface, so that the stem, as a whole, has a cylindrical form, and is thus very different from the conspicuously ribbed stem of *H. Grievii*. The comparison with the form of the stem in *H. tiliæoides* is difficult, as the cortex is never complete in the specimens of the latter species.

The inner cortex contains masses of dark sclerotic tissue, arranged in vertical series (see fig. 31), while the outer zone consists chiefly of sclerenchymatous fibres. There is thus nothing peculiar in the structure of the cortex; its appearance is somewhat unusual and suggestive of charring. The transverse section shows a fairly-preserved pair of leaf-trace bundles (fig. 30, *lt.*). The fact of their forming a pair suggests a comparison with *H. tiliæoides*, though this arrangement is not absolutely unknown in the other species.

A tetrarch root of the type which we have referred to *Heterangium*, lies close to the stem opposite an interruption in the cortex. It is not unlikely that it may have belonged to the plant (fig. 30, *Rt.*). Other roots of the same kind occur in the preparations.

We think it certain that this specimen does not belong to *H. Grievii*, or at least that it does not represent the ordinary form of stem in that species. We should have suggested that it might be a young specimen of *H. tiliæoides*, were it not for the want of exact agreement in the details of the primary wood. It is possible that it may represent some peculiar form of stem, such as a rhizome, belonging to one or other of the known species. If it is desirable to give the specimen a provisional name, we may speak of it as *H. cylindricum*, but without desiring to imply that its claims to specific distinctness are likely to hold good permanently.

III. AFFINITIES OF *Lyginodendron* AND *Heterangium*.

So long as we are without information as to the reproductive organs of these genera, it is evident that any discussion of their affinities must be conducted with the greatest caution. Considering, however, the very thorough knowledge of their vegetative parts which we now possess, we may reasonably hope to throw considerable light on the question, although we cannot yet solve it finally. Some encouragement in the attempt may be derived from the experience of palæobotanists in other families. In the case of the Lepidodendreæ, for example, there can, we think, be no doubt that an unprejudiced consideration of their vegetative structure alone is sufficient to lead to a true estimate of their relationships, which is only confirmed by our knowledge of their fructifications. So also with the Calamarieæ ; as we showed in a former paper,* a minute examination of the anatomical characters, especially those of the primary tissues, affords by itself the strongest presumption of Equisetaceous affinities, and so helps us to the right interpretation of the evidence from the fructifications.

A really accurate knowledge of vegetative characters, especially of those derived from the internal structure, may, we believe, be trusted to put us on to the right track in cases where the larger systematic groups are alone in question.

The fact that in various respects both *Lyginodendron* and *Heterangium* strongly resemble Ferns has been noticed since the first discovery of these plants, and has been demonstrated in the preceding pages. As regards the former genus, we have now proved beyond doubt that the highly compound leaves were those of a *Sphenopteris*, and in *Heterangium* the general character of the foliage was evidently similar. The external form and even the venation of the leaf, however, would by themselves carry no decisive weight, though hundreds of fossil species have been referred to the Ferns on no better grounds. But beyond this, the internal structure of the leaf is now well known in *Lyginodendron*, and to a less degree in *Heterangium*, and proves to be in all respects that of a Fern, as is shown most clearly by the concentric structure of the vascular bundles in the petiole and rachis. This fact holds good for both genera. Both in structure and form, then, the leaves of *Lyginodendron* and *Heterangium* are Fern-leaves, their one point of difference being the occurrence of pitted as distinguished from scalariform tracheides in their xylem.

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* WILLIAMSON and SCOTT, "Further Observations on the Organization," &c., Part I.

Now, as regards *Lyginodendron*, the distinctively Fern-like character is limited to the foliage; this, however, is not the case with the other genus. Apart from the secondary growth, the stem of *Heterangium* is essentially that of a monostelic Fern of the *Gleichenia* type. The resemblance of the stele of *Heterangium* to that of a *Gleichenia* is, in fact, very marked, as regards the distribution of the tracheides and conjunctive parenchyma, the position of the protoxylem-groups, and the presence of a wide pericycle. We think the comparison with *Gleichenia* may prove to be a fertile one, and hope to pursue it further on another occasion. It is not at all unlikely that the *Gleichenia* type of structure may be of great antiquity. We see, then, that if we left the secondary thickening out of account, there would be no serious reason against regarding *Heterangium* as a fairly typical monostelic Fern. We notice, however, certain peculiarities:

1. The presence of pitted tracheides.
2. The collateral structure of the bundles passing from the stele to the leaves.
3. The differentiation of the peripheral part of the stele into more or less distinct bundles continuous with the leaf-traces. The last named character is more marked in *H. tiliæoides* than in *H. Grievii.*

The occurrence of secondary thickening in a Fern-like plant is not in itself very surprising. We know that it takes place in a perfectly typical way, though not to any great extent, in the stems of *Botrychium* and *Helminthostachys* at the present day.

The question now arises, What is the relation between *Lyginodendron* and *Heterangium?* The latter, as we have seen, shows a great preponderance of Fern-like characters. This does not seem to be the case in *Lyginodendron*, in which the stem, apart from the leaves, suggests anything rather than a Fern. Yet the essential differences between the two genera are limited to their steles. In typical specimens of *Lyginodendron* the whole interior of the stele is occupied by pith, around which we find a ring of scattered bundles. The most remarkable point, however, is the exact agreement in structure between the bundles of *Lyginodendron* and the peripheral strands, which form part of the stele in *Heterangium*. We said, above, that a *Heterangium* might be regarded as a *Lyginodendron*, with the bundles connected together by medullary xylem. Conversely we might look on *Lyginodendron* as a *Heterangium* in which all the primary xylem except the peripheral strands has disappeared. It seems as if in *Lyginodendron*, which is probably the more advanced type, as it appears to be the later in geological origin, only that part of the primary vascular tissue is developed which is in direct connection with the leaves. All the rest has disappeared, having, perhaps, been sufficiently replaced by the newly acquired secondary tissues.

Platyzoma, one of the Gleicheniaceæ, resembles *Lyginodendron* in possessing a pith,[*] but the nearest analogy to *Lyginodendron* among recent Ferns is probably to be found in *Osmunda*, which has recently been investigated afresh by ZENETTI.[†] *Osmunda* is a monostelic Fern with a large pith, collateral bundles in the stem, and a concentric bundle in the petiole. The leaf-trace bundles, however, unlike those of *Lyginodendron*, become concentric immediately on leaving the stele. Another difference from the fossil genus is that in *Osmunda* the phloëm forms a continuous ring, which does not seem to have been the case with the primary phloëm of *Lyginodendron*. The position of the protoxylem is also different: in *Lyginodendron*, as we have seen, all bundles are mesarch, with the protoxylem-strands embedded in the primary wood nearer its outer than its inner surface. In *Osmunda* the bundles only have protoxylem at all in the upper part of their course.[‡] In the bundles, where they first enter the stele, the protoxylem lies on the inner concave side of the xylem horse-shoe. Lower down, where the horse-shoe becomes a closed curve, the protoxylem comes to be surrounded by wood, so that here we have a certain resemblance to the *Lyginodendron* bundle, though perhaps only an accidental one.[§]

The example of *Osmunda* is, at any rate, sufficient to show that the general primary structure of *Lyginodendron* is consistent with Fern affinities.

So far we have considered only the points in which our two genera approach the Ferns. We have now to call attention to the remarkable relation which their structure shows to that of Cycadeæ.

The secondary tissues strongly recall those of Cycads; the resemblance shows itself especially in the simple structure of the secondary wood, the great number of the medullary rays, and the tracheides with multiseriate bordered pits on their radial walls. The structure of the phloëm also agrees well with that of Cycadeæ, and in the case of *Heterangium tiliæoides* the agreement extends to the details of the sieve-plates. The rarity of the tangential divisions in the medullary rays, causing an apparent interruption of the cambium at these points, is another peculiarity which both our fossil genera share with Cycadeæ.[||]

So far as the secondary tissues are concerned, the Cycadean characters apply to both *Heterangium* and *Lyginodendron*, though, on the whole, more marked in the latter. The primary structure of the stele in *Heterangium* bears no resemblance to that of a Cycad, while in *Lyginodendron* the presence of a pith and distinct bundles create a certain similarity.

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[*] Some account of the anatomy of Gleicheniaceæ will be found in POIRAULT, "Recherches anatomiques sur les Cryptogames vasculaires," 'Ann. des Sci. Nat., Bot.,' Ser. 7, T. 18, p. 171, 1894.

[†] 'Botanische Zeitung,' 1895, Abth. 1, p. 53.

[‡] An interesting analogy for this is found in the fossil *Poroxylon*; see BERTRAND et RENAULT, "Recherches sur les *Poroxylons*," p. 283.

[§] See ZENETTI, *loc. cit.*, woodcut 2, p. 57, Plate 2, figs. 2 and 3.

[||] See DE BARY, "Comparative Anatomy," &c., p. 611.

The most interesting and remarkable point, however, which our investigations have brought to light, is the fact that the vascular bundles in the *stem* of *Lyginodendron* have exactly the same structure as those in the *leaf* of existing Cycads. This applies also to the leaf-traces and the bundles which form the outer part of the stele in *Heterangium*. Both in our fossil genera and in Cycadeæ the bundles in question are *collateral* and *mesarch*, the primary xylem being chiefly centripetal, while a smaller part is centrifugal. The essentially Cycadean structure of the bundles illustrated in Plates 21 and 22, figs. 2, 3, 4, 5, and 6 is evident to any botanist.

This type of bundles among existing plants is limited to Cycadeæ, and until now has only been observed in their leaves, in which it is of universal occurrence.*

Among fossil plants the same structure occurs most clearly in the leaves of Cordaiteæ,† and also in Cycadoxyeæ and *Sigillaria*, though, in the last case, the true interpretation of the structure is doubtful.‡ In the petiole of *Myeloxylon*, according to SEWARD, the xylem of the bundles appears to have been wholly centripetal, so that the agreement with Cycadeæ is here imperfect.§

Poroxylon, according to the investigations of MM. BERTRAND and RENAULT, appears to have had the Cycadean type of bundle in both stem and leaf.

We regard it as an essential characteristic of this type of bundles that the centrifugal, as well as the centripetal, portion of the xylem belongs to the *primary* tissue. This was certainly the case in the stem-bundles of both *Lyginodendron* and *Heterangium*, and the observations of one of us leave no doubt that the same holds good for the foliar bundles of recent Cycadeæ.

The occurrence of mesarch bundles in the stem of *Lyginodendron* and *Heterangium* at once suggests the view that this structure in Cycads is not a mere peculiarity of the leaf, but may rather be an ancestral character which once existed in the stem also, but has disappeared from that organ (in relation, perhaps, to the progress of secondary growth), while it has survived in the leaf.

These considerations suggested to one of us (D. H. SCOTT) the question whether some traces of this structure may not still exist in the stems of recent Cycadeæ. A preliminary investigation of this point has yielded the interesting result that, in the peduncles of both male and female flowers of *Stangeria*, the bundles are often mesarch. There is in these cases a well-marked centripetal xylem, in addition to the normal centrifugal portion of the wood. A full account of these observations will be published on another occasion.

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* The foliar bundle of *Isoëtes* is somewhat similar, but not identical.

† RENAULT, "Structure comparée de quelques tiges de la Flore Carbonifère," Clichy, 1879, Plate 16, figs. 2–8.

‡ RENAULT, *loc. cit.*, Plate 12, figs. 1, 2, and 6. See, however, SOLMS-LAUBACH, "Fossil Botany," chap. xi.

§ SEWARD, "On the Genus *Myeloxylon*," 'Annals of Botany,' vol. 7, 1893.

MM. Bertrand and Renault have expressed on purely theoretical grounds a somewhat similar view of the origin of the Cycadean type of bundle, and they also have cited *Lyginodendron* for comparison, relying not on any original investigations but on the figures published in Williamson's Memoir IV. They have, however, misunderstood the structure, owing to their assumption that the whole of the centrifugal wood is secondary and the whole of the primary wood centripetal. This, as we have shown, is not in accordance with the facts. It is, to a great extent, in consequence of this error that they are led to derive *Lyginodendron* and *Heterangium*, as well as their own genus *Poroxylon*, from Lycopodiaceæ, a conclusion which, as regards the genera investigated by us, is completely negatived by the whole organization of the leaf, while it is quite unnecessary as an explanation of the stem-structure.*

In *Lyginodendron* then, we have this remarkable combination of anatomical characters, namely, collateral, mesarch Cycadean bundles in the stem, passing over into concentric Fern-bundles in the petiole. In *Heterangium* we have the further complication, that the mesarch bundles in the lower part of their course occupy the periphery of a pithless stele, the whole interior of which consists of wood.

We wish to add one word as to the roots; we have called attention above to their great similarity, when young, to Marattiaceous roots, and to their regular mode of secondary growth recalling that of a typical Dicotyledon. They are less similar to roots of Cycads than we might have expected, but then we must remember that Cycadean roots are generally fleshy, and consequently much modified in structure. We may reasonably regard the roots of *Lyginodendron* and *Heterangium* as those of Fern-like plants, which have already thoroughly adapted themselves to secondary growth by means of a cambium. Certainly they bear no resemblance whatever to any known roots of Lycopodiaceæ.

We have seen how extraordinary a combination of characters belonging to various groups these genera present. In different parts of their structure they have been found to present points in common with Gleicheniaceæ, Osmundaceæ, Marattiaceæ, Ophioglosseæ, and Cycadeæ.

The view of the affinities of *Lyginodendron* and *Heterangium*, which we desire to suggest, is, that they are derivatives of an ancient and "generalized" (or rather non-specialized) Fern-stock, which already show a marked divergence in the Cycadean direction. Of the two genera *Heterangium* appears to be the more ancient, and certainly stands nearer to the Filicinean ancestry. *Lyginodendron*, while still retaining conspicuous Fern-like characters, has advanced much further on Cycadean lines.

We do not intend to suggest that in these plants we have the actual ancestors of existing Cycadeæ. The search for "missing links" has met with little encouragement of late years, and we now realize how much the chances are against our lighting on the direct ancestors of living forms. We believe, however, that in *Lyginodendron* and *Heterangium* we have examples of Fern-like plants of a primitive type, which have undergone modifications of the same kind as those to which the Cycadeæ owed their origin.

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* Bertrand et Renault, "Remarques sur les faisceaux foliaires des Cycadées actuelles," &c., 'Arch. Bot. du Nord de la France,' 3rd année, No. 35, 1886, p. 237. "Recherches sur les *Poroxylons*," *loc. cit.*, p. 382, &c.

How far, in the case of these genera, such modification had proceeded cannot be determined until their reproductive organs have been found. Possibly these plants had only varied in their vegetative characters and still retained an essentially Fern-like fructification; possibly, on the other hand, they had already acquired some Gymnospermous type of reproductive organs. As to all this we know nothing. All we can say is, that such divergence from a Fern-type, as is actually shown by the known characters, is distinctly in a Cycadean direction.

Our view as to *Lyginodendron* and *Heterangium* is in essential agreement with that of Count SOLMS-LAUBACH, who has described in *Protopitys Bucheana* another of these types, intermediate between Filicineæ and Gymnosperms.*

We think it very probable that *Poroxylon*, so beautifully investigated by MM. BERTRAND and RENAULT, will find its place in a similar intermediate position. In many respects the similarity of structure between this genus and *Lyginodendron* is quite unmistakable, extending even to minute anatomical details, and we think it not unlikely that the agreement may turn out to be even closer than appears from the statements of the authors. *Poroxylon* certainly approaches Cycads more closely than *Lyginodendron* does. SEWARD'S *Rachiopteris Williamsoni*,† as well as *Myeloxylon*, must probably be added to the list. As to *Sigillariopsis*, we prefer not to express any opinion.

We think the existence of a fossil group on the borderland of Ferns and Cycadeæ is now well established. The relation of these forms to those very ancient Gymnosperms, the Cordaiteæ, is a difficult and most interesting question, which cannot, however, be discussed here.‡

The photographic illustrations to the present paper (Plates 18–20) are the work of the late Mr. W. KIRMAN, formerly of the Royal College of Science, London. The camera-lucida drawings, reproduced in Plates 21–29, like those in our former joint papers, were made by Mr. GEORGE BREBNER.

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* 'Bot. Zeitung,' 1894, Abth. 1, p. 206.

† 'Ann. of Bot.,' vol. 8, 1894.

‡ NOTE.—In Memoir IX. (p. 352, Plate 25, figs. 90–92) a remarkable piece of stem from the volcanic ash of Arran was described under the provisional name of *Lyginodendron* (?) *anomalum*. We have nothing to add, except that we do not now think the fragment has anything in common with the genus *Lyginodendron*, and would rather suggest a comparison with a *Cycadeoxylon*, figured by M. RENAULT ("Structure comparée de quelques tiges," &c., Plate 14).

NOTE, ADDED DECEMBER 19, 1895.

In 1869 M. RENAULT described two specimens from the upper coal-measures of Autun, under the names of *Lycopodium punctatum*, B. Ren., and *Lycopodium Renaultii*, Ad. Br. ('Ann. des Sci. Nat.' (Bot.), Sér. 5, T. 12, pp. 178–185, Plates 12–14). M. RENAULT now kindly informs me that in the text of his 'Flore fossile du bassin houiller et permien d'Autun et d'Épinac,' Part 2, which I have not yet had an opportunity of seeing, he has transferred these fossils to the genus *Heterangium*. I had already convinced myself, by comparison of his figures with our specimens, that this was their proper position. The plants in question have nothing in common with *Lycopodium*, for the structures described as leaf-traces in the memoir of 1869 are not really of that nature. Those shown in the inner part of their supposed course probably represent medullary rays, while those in the cortex are certainly identical with the sclerotic bands so often figured and described from the English specimens. (See our figs. 22, 28, and 31; WILLIAMSON, Part IV., figs. 32, 45, &c.)

The agreement in structure with our own species of *Heterangium* is remarkably close. M. RENAULT'S *H. punctatum* is much like our *H. tiliæoides*, while *H. Renaultii* recalls the specimen which we provisionally term *H. cylindricum*. The genus *Heterangium* evidently had a great vertical range in the carboniferous formation.—D. H. SCOTT.

EXPLANATION OF PLATES.

Plates 18–20. Lyginodendron Oldhamium. *Photographs by the late* Mr. W. KIRMAN, *from the actual sections. Many require to be examined with a lens.*

PLATE 18.

Photograph 1. Transverse section of a medium-sized stem passing through an internode. The outer, or *Dictyoxylon* cortex is perfect; the inner cortex only remains here and there, especially on the left. *l.t.*^{1}–*l.t.*^{5}, the five leaf-traces in the pericyle, numbered in order from within outwards. Note that *l.t.*^{1} is a single bundle, the rest more or less double (*l.t.*^{5} accidentally displaced); *w.*^{1}–*w.*^{5}, the perimedullary xylem-strands alternating with the external bundles; they are numbered according to the leaf-traces on their anodic side. Between *w.* and *l.t.* are the secondary wood and the phloëm. Compare Plate 21, fig. 1, and for details see Plates 21 and 22, figs. 2, 3, 5, 6 and 7. × 6½. C.N. 1640 (see p. 706).

Photograph 2. Transverse section of a young stem at the commencement of secondary growth. *d.c.*, *Dictyoxylon* cortex; *l.t.*^{1}, the innermost of the four leaf-traces;

the remaining three are double; *w.*, one of the six perimedullary strands of xylem. Between *w.* and *l.t.* a thin zone of secondary wood is seen. The external layer of cortex to the right is not evidently connected with this stem. × 11. C.N. 1144D (see pp. 710 and 714).

Photograph 3. Part of transverse section of a stem, showing the base of a petiole in connection with it. *st.*, stem; *pt.*, petiole. The petiole contains a double bundle, which is concentric. Plate 19, photograph 8A, and Plate 23, fig. 10 show other sections of the same specimen. × 3. C.N. 1980 (see p. 725).

Photograph 4. Radial section of stem and petiole, showing the connection between them. *d.c.*, *Dictyoxylon* cortex of stem; *pc.*, pericycle; $x.^2$, secondary wood; *p.*, pith; *pt.*, petiole, cut off at this point; *sc.*, axillary sclerotic band; *c.*, outer limit of cortex of petiole; *lt.*, leaf-trace bundle, entering petiole from stem. × $3\frac{1}{2}$. C.N. 1982 (see p. 725).

Photograph 5. Transverse section of a small secondary branch of a petiole. The outer cortex has the usual *Dictyoxylon* structure; *s.s.*, secretory sacs of the inner cortex; *v.b.*, the concentric vascular bundle with V-shaped xylem completely surrounded by phloëm. × about 35. C.N. 145 (see p. 728).

Photograph 6. Transverse section of part of the lamina, cut through a number of leaflets just separating from one another. A part of one of the leaflets is displaced and seen in obliquely superficial view. × about 35. C.N. 1885D (see p. 727).

PLATE 19.

Photograph 7. Vertical section of a leaflet. *p.p.*, palisade parenchyma; above this is the hypoderma, and then the epidermis; *s.p.*, spongy parenchyma; *v.b.*, vascular bundle, in obliquely longitudinal section. On the under side of the leaf is an outgrowth, perhaps of the same nature as the cortical emergences. × about 70. C.N. 1196 (see p. 730).

Photograph 8. Part of a transverse section of a large stem, passing through the base of an adventitious root. *rt.*, outer limit of cortex of root; *cy.*, central cylinder of root, which has formed secondary wood; *tr.*, tracheides connecting the base of the root with the wood of the stem; *x.*, remains of primary wood of stem; $x.^2$, its secondary wood; *pd.*, periderm; *d.c.*, *Dictyoxylon* cortex; *l.t.*, large leaf-trace bundle. × about 12. C.N. 1144B (see p. 733).

Photograph 8A. Another section of the same specimen as photograph 3, taken higher up. *st.*, stem; *pt.*, petiole. Note the dark axillary band at the junction of the two. At *rt.* a root is seen in longitudinal section, passing out from the wood through the cortex. × 3. C.N. 1981 (see pp. 725 and 734).

Photograph 9. Part of tangential section of the cortex of a large stem, showing base of adventitious root; *l.t.*, leaf-trace bundle of stem; *d.c.*, part of the *Dicty-*

oxylon cortex; *rt.*, outer limit of cortex of root; *cy.*, its central cylinder, with abundant secondary wood. × about 15. C.N. 1883 (see p. 734).

Photograph 10. Another root from the same preparation; it has just become free from the stem, part of the cortex of which is seen at *d.c.* *c.*, *c.*, cortex of root; *cy.*, middle of its central cylinder; *br.*, *br.*, two rootlets arising from the root. × 28. C.N. 1885 (see p. 734).

PLATE 20.

Photograph 11. Transverse section of a young root, before secondary growth has begun. *c.*, cortex of root; *e.c.*, external cortical layer; *cy.*, the pentarch stele, in which the alternating xylem and phloëm-strands are seen. The cortex is full of secretory sacs. × about 30. C.N. 1634 (see p. 736).

Photograph 12. Transverse section of a root branching. *br.*, *br.*, two rootlets, arising opposite two of the protoxylem-groups, of which there are six in all, two being lettered *px.*; $x.^2$, secondary wood, beginning to form between the protoxylem-groups. × about 30. C.N. 1899 (see pp. 738 and 740).

Photograph 13. Transverse section of a pentarch root, with secondary thickening. *px.*, the five protoxylem-groups, to each of which a ray corresponds; *ph.*, a phloëm-group; $x.^2$, secondary wood; *cb.*, cambium; *c.*, outer limit of cortex. × about 30. C.N. 1631 (see p. 739).

Photograph 14. Transverse section of a very advanced tetrarch root. *px.*, the four protoxylem-groups; *ph.*, a phloëm-group, in which the primary phloëm is very distinct; $x.^2$, secondary wood; *cb.*, cambium; *c.*, outer limits of cortex. × about 20. C.N. 1632 (see p. 739).

Photograph 15. Longitudinal median section of a root, giving off two rootlets. *br.*, *br.*, the two rootlets; *c.*, cortex of main root; *x.*, xylem of its stele. × about 12. C.N. 1899A (see p. 740).

Plates 21–29.—*Figures from camera-lucida drawings by* Mr. GEORGE BREBNER.

Plates 21–25.—Lyginodendron Oldhamium.

PLATE 21.

Fig. 1. Transverse section of a very well-preserved stem. The *Dictyoxylon* cortex shows dilatation conspicuously. Next comes the inner cortex. *pd.*, periderm, at outer limit of pericycle; $lt.^1$–$lt.^5$, five leaf-traces passing through the pericycle, numbered in order from within outwards; their arrangement corresponds to a $\frac{2}{5}$ phyllotaxis; *ph.*, one of the primary phloëm-groups; secondary phloëm and cambium shown; within these is the wide secondary wood; *x.*, one of the eight perimedullary xylem-strands; pith and

pericycle contain numerous sclerotic groups. × 6. From a new specimen (in the possession of D. H. SCOTT), obtained through Professor BOWER, F.R.S., from Oldham (see pp. 706 and 708).

Fig. 2. Part of transverse section from the same specimen as Plate 18, photograph 1, showing the xylem-strand marked *w.*[2] in that photograph. The mesarch structure is evident. *px.*, protoxylem; *x.*, centripetal portion of primary wood; *x.*[1], centrifugal portion of the same; *x.*[2], part of secondary wood; *r.*, *r.*, rays; *p.*, *p.*, pith; *s.s.*, secretory sac. × 100. C.N. 1884 (see pp. 709 and 712).

Fig. 3. Another section from the same specimen, showing the large double xylem-strand, marked *w.*[5] in photograph 1. Lettering as in fig. 2. × 100. C.N. 1640 (see pp. 709, 711, and 712). (C.N. 1640 and 1884 are adjacent and practically identical sections from the same stem.)

PLATE 22.

Fig. 4. Part of a radial section, passing through one of the primary xylem-strands, and showing mesarch structure. Lettering as in figs. 2 and 3. × 100. C.N. 1982 (see p. 712).

Fig. 4A. Parts of secondary tracheides from same section, to show bordered pits. × 150.

Fig. 4B. Ditto in tangential section. *r.*, secondary rays. × 150. C.N. 1985 (see p. 716).

Fig. 5. Part of transverse section showing the leaf-trace bundle, marked *l.t.*[1] in photograph 1, illustrating the collateral mesarch structure. *px.*, *px.*, the two protoxylem-groups of the bundle; *x.*, centripetal part, *x.′*, centrifugal part, of its primary wood; *x.″*, secondary wood of bundle; *cb.″*, its cambium; *ph.″*, its phloëm; *x.*[2], secondary wood of the stem; *cb.*, cambium; *ph.*[2], phloëm; *s.s.*, secretory sacs; *pd.*, periderm, at outside of pericycle. × 70. C.N. 1640 (see pp. 709 and 712).

Fig. 6. Transverse section through the leaf-trace bundle, *l.t.*[2], of photograph 1. At this level the bundle has become double, and is without secondary tissues. The structure is exactly that of foliar bundles in Cycadeæ, *e.g.*, *Stangeria*. Lettering as in fig. 5. × 70. C.N. 1884 (see pp. 709 and 713).

Fig. 7. Part of transverse section from the same specimen, to show cambium and phloëm. *x.*[2], secondary wood; *r.*, *r.*, rays; *cb.*, cambium; *ph.*[2], secondary phloëm; *ph.*, primary phloëm; *s.s.*, secretory sacs in pericycle; *pd.*, periderm. × 70. C.N. 1640 (see p. 715).

Fig. 7A. Part of a tangential section through the secondary phloëm. *ph.*[2], strands of sieve-tubes and elongated parenchyma; *r.*, *r.*, phloëm-rays; *hy.*, branched fungal hypha. × 70. From one of the new Oldham specimens (D. H. S.) (see p. 716).

PLATE 23.

Fig. 8. Part of a transverse section to show anomalous secondary tissues in the pith, *x*^{2}., normal secondary wood; *r.*, *r.*, rays; *px.*, protoxylem of normal primary xylem; *x.*, centripetal, *x.′*, centrifugal, part of primary xylem; *x.*^{3}, anomalous medullary wood; *cb.*^{3}, anomalous cambium; *ph.*^{3}, anomalous phloëm; *p.*, *p.*, pith. × 70. C.N. 1190 (see p. 722).

Fig. 9. Part of a transverse section, to show a leaf-trace bundle in the intermediate position between pith and pericycle. *lt.*, leaf-trace, with a large fan of secondary tissue; *ph.*, phloëm of the leaf-trace, continuous on the left with the phloëm-zone (*ph.*^{2}) of the stem; *x.*^{2}, secondary wood of stem; *x.*^{3}, *x.*^{3}, patches of anomalous wood in trace-gap; *p.*, *p.*, pith; *pd.*, periderm. × 14. From one of the new Oldham specimens (D. H. S). (see p. 710).

Fig. 10. Part of a transverse section, to show petiole in connection with the stem. From the same series as photographs 3 and 8A, and intermediate between them. *pt.*, petiole; *f.b.*, its double bundle; *sc.b.*, sclerotic axillary band (*cf.* photograph 4); *d.c.*, Dictyoxylon cortex of stem; *lt.*, part of a leaf-trace bundle; *x*^{2}., secondary wood. × 7. Slide 56 (D. H. S.) (see p. 725).

Fig. 11. Obliquely longitudinal section of the *same petiole*, when it has become free from the stem. *pt.*^{2}, branch of the petiole; *f.b.*, *f.b.*, vascular bundles of main and branch petioles; *c.*, outer cortex; *i.c.*, inner cortex; *e.*, *e.*, cortical emergences. × 6⅓. C.N. 1979 (see p. 725).

Fig. 12. Part of outer cortex of a petiole, to show an apparently glandular emergence. *sc.*, sclerenchyma of cortex; *e.*, emergence; *g.*, supposed glandular tissue. × 100. C.N. 139 (see p. 730).

Fig. 13. Part of a longitudinal section of a petiole, passing through the bundle, of which about half is shown. *px.*, protoxylem; *x.*, centripetal, *x.′*, centrifugal, part of xylem; *ph.*, phloëm; *c.*, cortical tissue. × 70. C.N. 1985 (see p. 728).

PLATE 24.

Fig. 14. Radial section through a bud-like structure. *ax.*, hollow axis of the whole structure; *e.*, *e.*, outgrowths, resembling the cortical emergences of *Lyginodendron*. × 20. C.N. 1859 (see p. 732).

Fig. 15. Tangential section of the same. *e.′*, bases of the outgrowths. × 20. C.N. 1858.

Fig. 16. Leaflet in vertical section. *ep.*, epidermis; *h.*, hypoderma; *p.t.*, palisade tissue; *s.t.*, spongy tissue; *v.b.*, vascular bundles, the one in transverse, the other in longitudinal, section. × 100. C.N. 1197 (see p. 730).

Fig. 16A. From a section of another leaflet, to show a stoma on the lower surface. *s.t.*, part of the spongy tissue; *ep.*, epidermis; *s.c.*, prominent subsidiary cells; *g.c.*, depressed guard-cells of the stoma. × 500. C.N. 1197 (see p. 731).

Fig. 17. Transverse section of *the same root, rt.*[3], which in figs. 18 and 18A is seen in connection with a stem of *Lyginodendron.* This is from a third section of the specimen, where this root has become free. Note its typical *Kaloxylon* structure. *px.*, *px.*, two of the seven protoxylem-groups; *x.*, primary wood; *x.*[2], secondary wood; *ph.*, phloëm; *c.*′, inner cortex; *c.*, outer cortex, or epidermal layer. × 30. C.N. 1885B (see p. 734).

PLATE 25.

Fig. 18. Oblique section of a stem of *Lyginodendron,* showing roots (= *Kaloxylon Hookeri*) in connection with it. *rt.*[1] and *rt.*[2], two free roots; *rt.*[3] and *rt.*[4], two roots in connection with the stem; *r.x.*, part of xylem of *rt.*[3], traversing cortex of stem; *br.*, rootlet given off by *rt.*[4]; *rt.*[5], base of a fifth root, at its junction with wood of stem; *d.c.*, *Dictyoxylon* cortex of stem; *x.*[2], its secondary wood; *p.b.*, primary xylem-strands. *Cf.* fig. 17. × 6. C.N. 1885A (see p. 734).

Fig. 18A. Another section of the same specimen. All the four roots, *rt.*[1]–*rt.*[4], are shown; *rt.*[1] and *rt.*[2] remain free, *rt.*[3] and *rt.*[4] are here seen in obliquely longitudinal section; *r.x.*, xylem of roots; that of *rt.*[4] can be traced through cortex of stem. Lettering as before. × 6. C.N. 1885C (see p. 734).

Fig. 19. Part of a radial section of a root, to show position of protoxylem. *px.*, protoxylem; *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *pc.*, *en.*, probable pericycle and endodermis; *s.s.*, secretory sacs in cortex. × 100. C.N. 1633 (see p. 736).

Fig. 20. Part of a transverse section of a hexarch root, at the commencement of secondary growth; *px.*, three of the protoxylem-groups. That to the left is connected with the base of a rootlet. *x.*, *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *ph.*, three phloëm-groups, alternating with the protoxylem; *cb.*, cambium, just beginning its activity opposite the phloëm-groups; *en.*, endodermis. × 100. C.N. 1631 (see pp. 736 and 739).

Plates 26 *and* 27.—Heterangium Grievii.

PLATE 26.

Fig. 21. Transverse section through a young stem giving off a branch, *br.* *pc.*, pericycle of main stem, enclosing the stele; *l.t.*, *l.t.*, leaf-trace bundles; *i.c.*,

inner cortex; *sc.*, sclerotic masses seen in both stem and branch; *d.c.*, outer cortex of stem and branch; *cy.*, stele of branch, with commencement of secondary wood. × 8. C.N. 1915N (Dulesgate) (see pp. 745 and 753).

Fig. 22. Somewhat oblique, longitudinal section of a stem, showing the bases of two petioles, *pt.*; the left-hand petiole is seen in nearly radial section. *cy.*, stele of stem; *i.c.*, inner cortex, which in both petiole and stem is marked by the transverse sclerotic bands; *d.c.*, outer, or *Dictyoxylon* cortex. × 2¼. C.N. 1286 (Burntisland) (see p. 754).

Fig. 23. Fragments of foliage from another section of the same block. Portions of petioles, *pt.*, of all sizes, are shown, characterized by the cortical structure. At *l.* are fragments of leaflets; *sm.*, a fern-sporangium. × 14. C.N. 1287 (Burntisland) (see p. 755).

Fig. 24. Part of a transverse section of a stem, showing one of the primary xylem-strands at the periphery of the stele. *px.*, protoxylem; *x.*, centripetal, $x.^1$, centrifugal, part of xylem; *mx.*, metaxylem, which extends through the whole interior of the stele; *c.p.*, conjunctive parenchyma; $x.^2$, secondary wood; *cb.*, cambium; $ph.^2$, secondary phloëm. × 200. C.N. 1293 (Burntisland) (see pp. 748 and 751).

Fig. 25. Radial section through the corresponding region of another stem, to show the mesarch structure of the xylem-strand. $x.^2r.$, ray belonging to the secondary wood. Other lettering as in previous figure. Note the well-preserved bordered pits of the centripetal xylem. × 200. C.N. 1266 (Burntisland) (see pp. 748 and 751).

PLATE 27.

Fig. 26. Part of a transverse section of a stem, showing a collateral leaf-trace bundle, just separating from the stele. *px.*, *px.*, probable position of the protoxylem-groups; *x.*, centripetal, *x.*′, centrifugal, part of xylem of bundle; *ph.*′, its phloëm; $x.^2$, secondary wood of stem; $ph.^2$, phloëm; *pc.*, pericycle; *c.*, inner cortex. × 70. C.N. 1253 (Burntisland) (see p. 750).

Fig. 27. Transverse section of a tetrarch root, probably belonging to *H. Grievii*. *px.*, *px.*, two of the four protoxylem-groups, at the corners of the massive primary wood; $x.^2$, secondary wood; *cb.*, cambium; *ph.*, phloëm; *c.*′, inner cortex; *c.*, outer cortex, or epidermal layer. × 40. C.N. 1915R (Dulesgate) (see p. 758).

Fig. 28. Radial section of a stem, bearing three adventitious roots, *Rt.* *r.x.*, xylem of root, connected with that of stem; $x.^2$, secondary wood of stem, chiefly developed near bases of roots, and partly seen in transverse section; *x.*, primary wood of stem; *pc.*, pericycle; *sc.*, sclerotic masses, the only remains of the cortex. × 15. C.N. 1915G (Dulesgate) (see p. 756).

Fig. 29. Part of transverse section of a stem, showing what is probably a young adventitious root (*Rt.*) enclosed in the cortex. The supposed root has a definite stele. *c.*, its outer cortex, or epidermal layer; *d.c.*, part of the *Dictyoxylon* cortex of stem; *ph.*, phloëm; *x.*^{2}, secondary wood. × 50. C.N. 1915 (Dulesgate) (see p. 757.)

PLATE 28.

Figs. 30 and 31. *Heterangium sp.*

Fig. 30. Transverse section of stem. *cy.*, stele; *x.*, tracheides of the xylem which occupies the whole interior; *x.*^{2}, secondary wood, not much developed; *ph.*, remains of phloëm; *sc.'*, sclerotic nests in pericycle; *c.*, cortex; *sc.*, sclerotic cortical mass; *lt.*, pair of leaf-trace bundles; in the left hand one, xylem, *x.*, and phloëm, *ph.'*, can be distinguished; *Rt.*, a tetrarch root, perhaps connected with the stem; *br.*, rootlet. × 18. C.N. 1304A (see p. 764).

Fig. 31. Part of the longitudinal section of the same specimen. Lettering as before. The scale is too small to show the details of the tracheides, which have crowded bordered pits. × 18. C.N. 1304B (see p. 764).

Figs. 32 and 33. *Heterangium tiliæoides.*

Fig. 32. Part of a transverse section of a stem, showing portions of the primary and secondary wood. *px.*, protoxylem of one of the peripheral xylem-strands of the stele; *x.*, its centripetal, *x.'*, its centrifugal, primary xylem; *mx.*, metaxylem, which extends all through the interior of the stele; *c.p.*, conjunctive parenchyma; *x.*^{2}, secondary wood; *r.'*, *r.'*, the two principal rays, limiting the bundle; *r.*, *r.*, secondary rays. × 70. C.N. 1619 (see p. 760).

Fig. 33. Part of transverse section of another stem, showing mesarch xylem-strand more in detail. Lettering as before. Note the pitting on the walls of the primary tracheides. × 150. C.N. 1301 (see p. 760).

PLATE 29. *Heterangium tiliæoides.*

Fig. 34. Part of radial section of another stem passing through the corresponding region and showing the position of the protoxylem, *px.* (here much disorganized) in the xylem-strand. Lettering as in last two figures. × 150. C.N. 1628 (see p. 760).

Fig. 35. Another part of the same transverse section as fig. 32, to show cambium and phloëm. *x.*^{2}, secondary wood; *r.'*, principal ray; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*^{2}, secondary phloëm; *ph.*, primary phloëm; *pc.*, pericycle. × 70. C.N. 1619 (see p. 761).

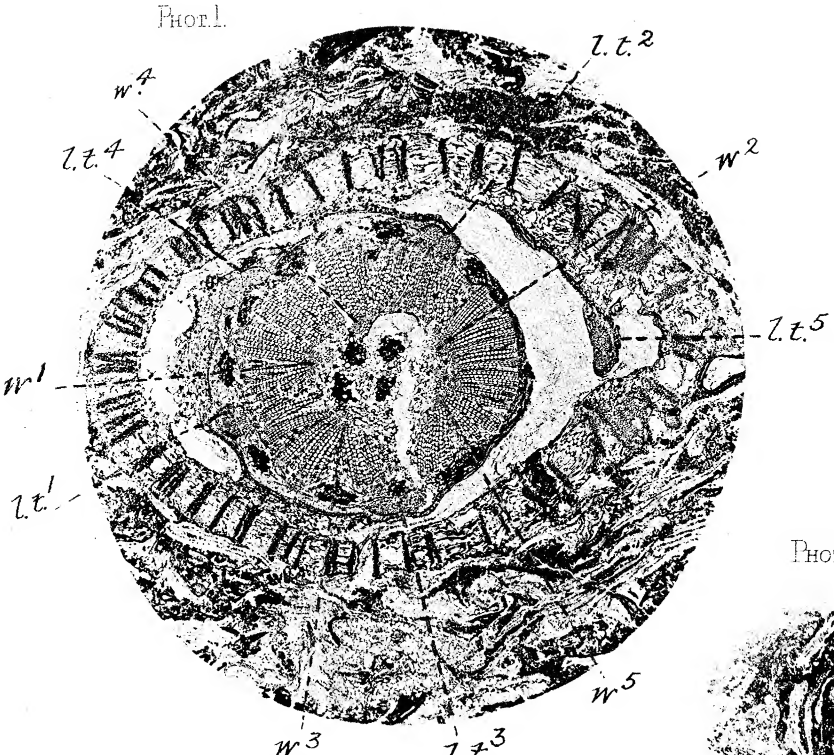
Fig. 36. Small part of transverse section of another stem, specially good for cambium. *x.*^{2}, strand of secondary wood; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*^{2}, secondary phloëm. × 150. C.N. 1302 (see p. 761).

Fig. 37. Part of the same radial section as fig. 34, to show developing wood, cambium, and phloëm. *x.*^{2}, secondary wood; *tr.*$'$, fully developed tracheides with bordered pits; *tr.*, developing tracheide with primordial pits only; *cb.*, cambium; *ph.*^{2}, secondary phloëm; *s.v.*, sieve-tube; *s.v.p.*, compound sieve-plate (also visible at other places); *r.*, secondary phloëm-ray. × 150. C.N. 1628 (see p. 761).

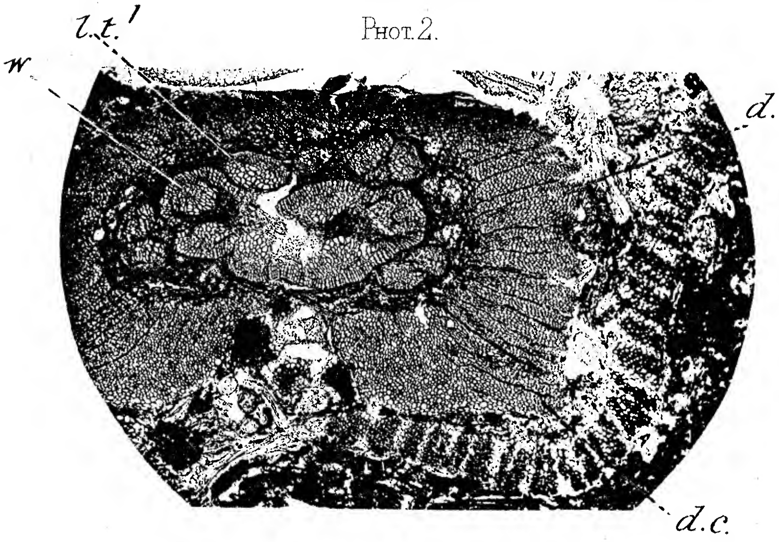
Fig. 38. Oblique longitudinal section through phloëm of another stem. *r.*, *r.*, phloëm-rays; *s.v.*, sieve-tubes; on several of the walls the sieve-plates are evident. × 150. C.N. 1304 (see p. 762).

Fig. 38A. Part of a sieve-tube enlarged from the previous section, at *a*, showing the sieve-plates, *s.v.p.* × 500. C.N. 1304 (see p. 762).

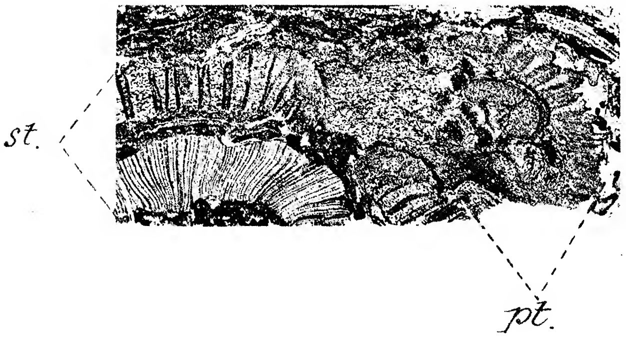
Phot. 1.



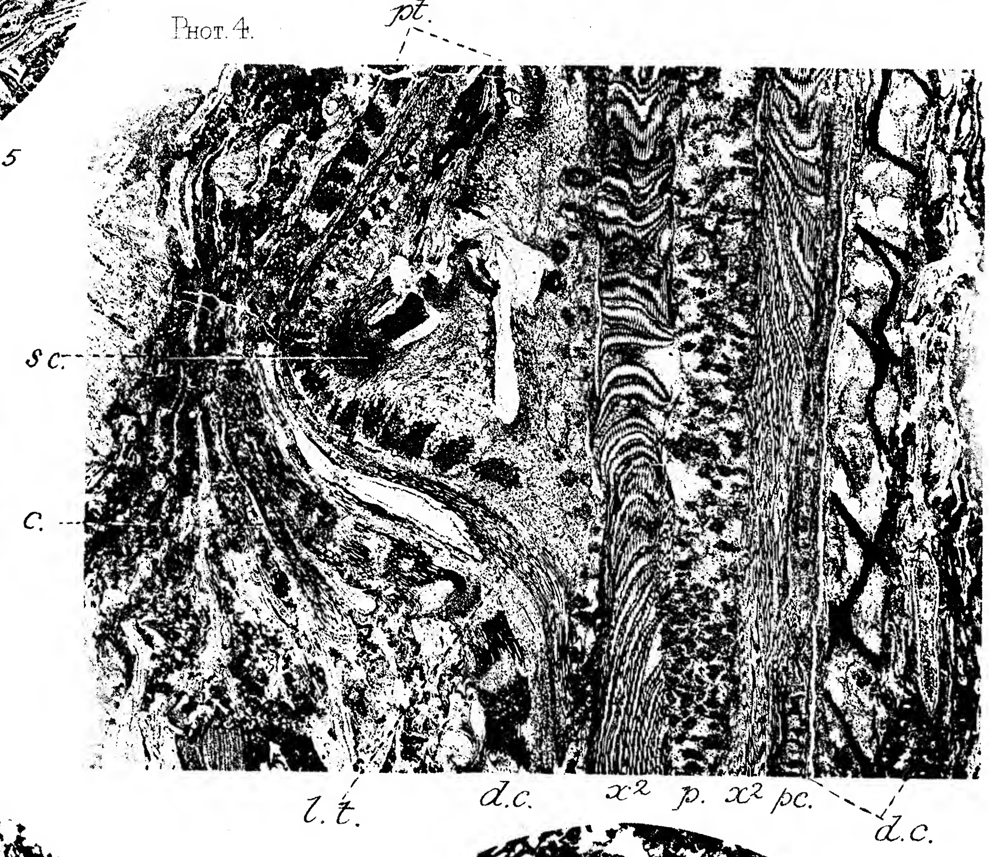
Phot. 2.



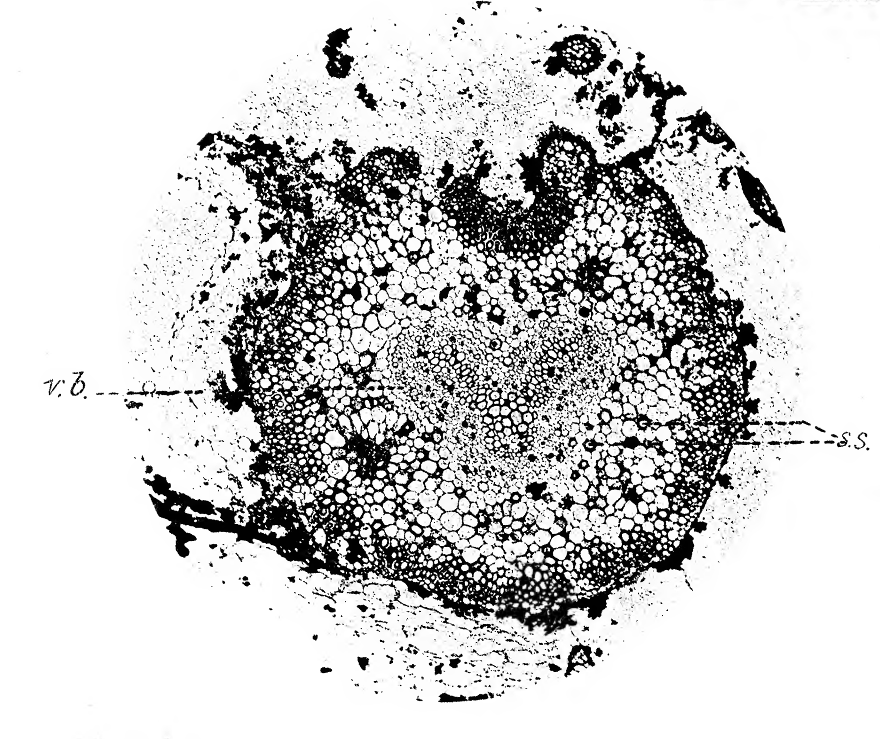
Phot. 3.



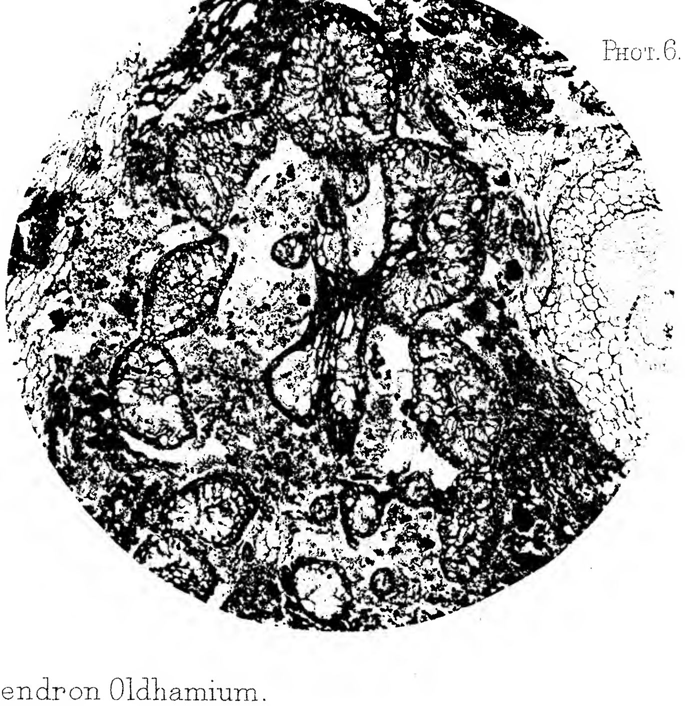
Phot. 4.



Phot. 5.



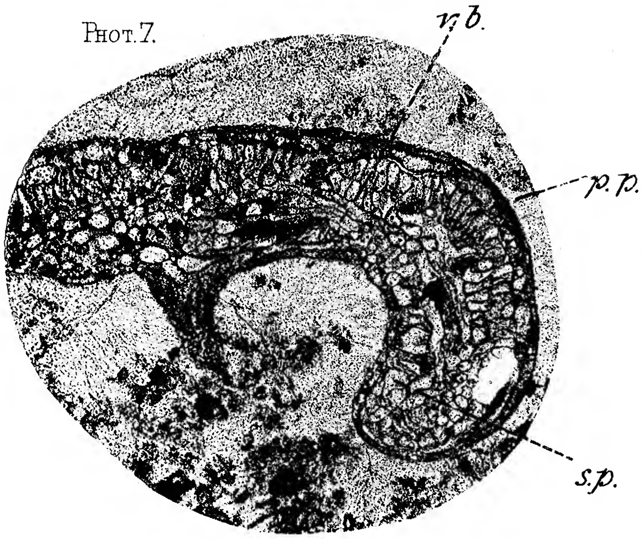
Phot. 6.



W. Kirman. Photo.

Photographs 1–6, Lyginodendron Oldhamium.

Phot. 7.



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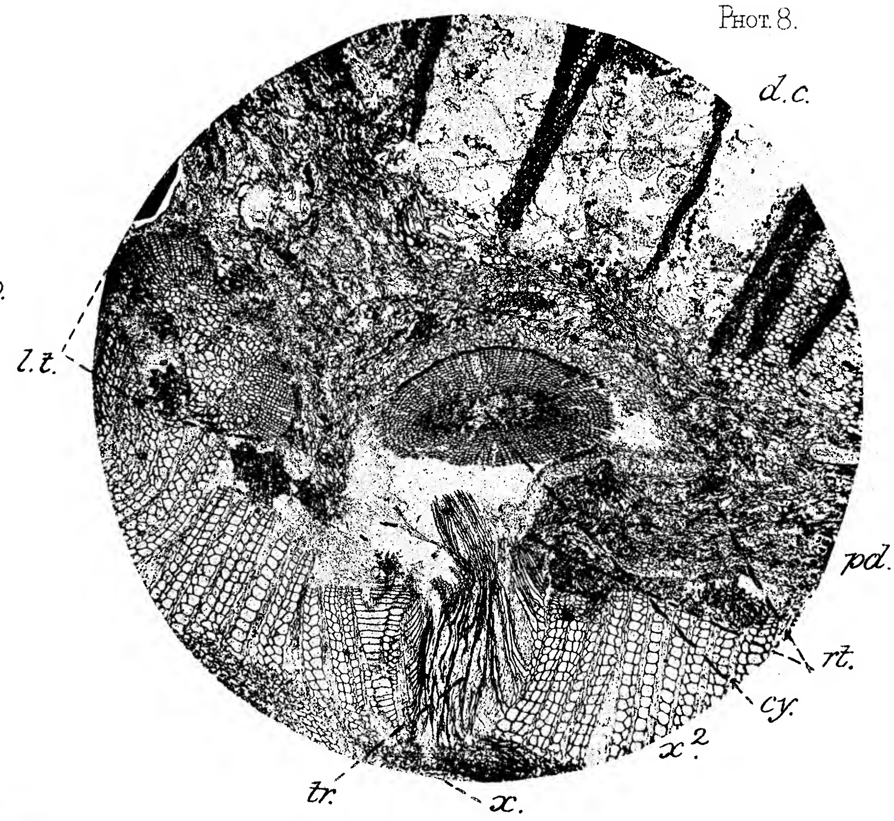

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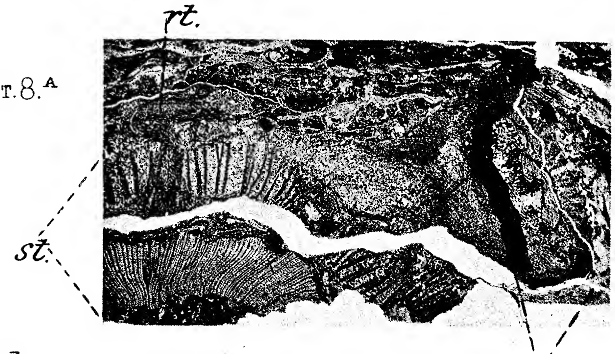

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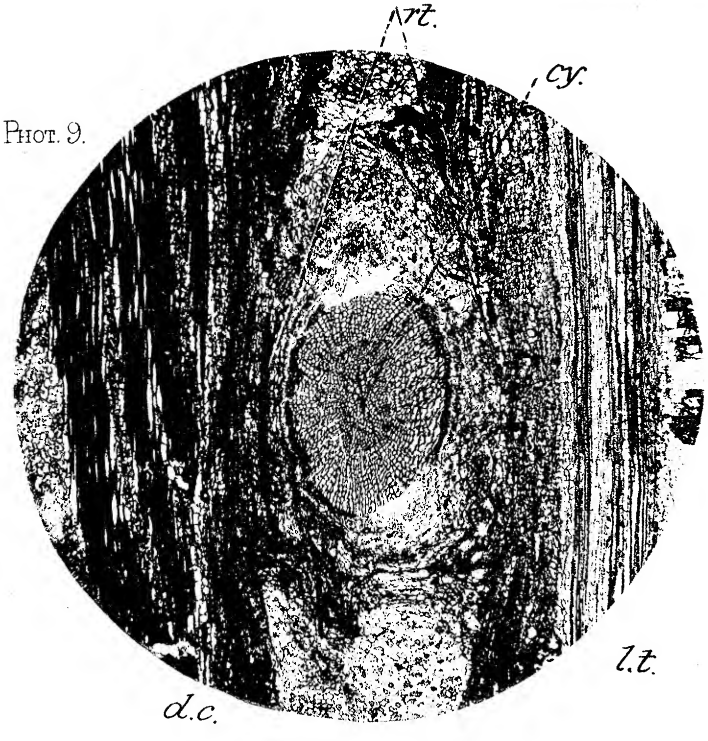

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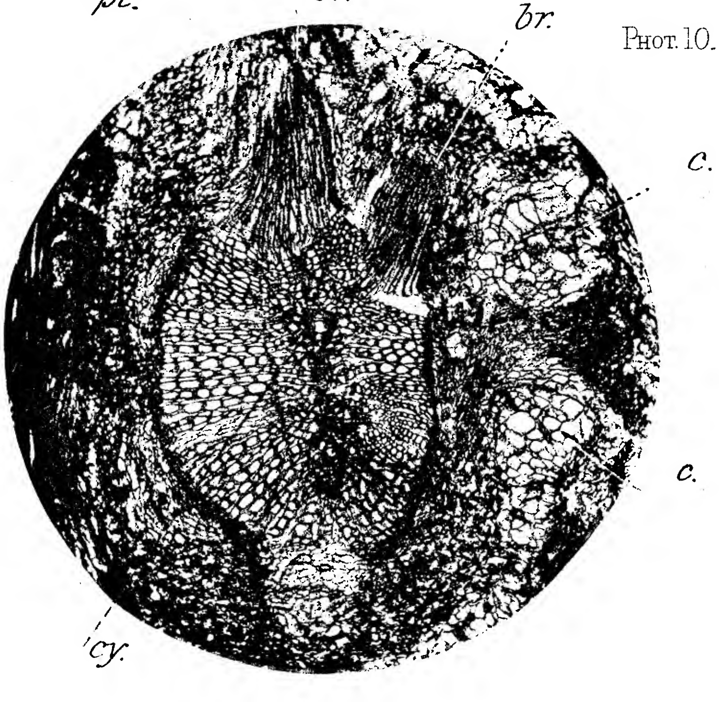
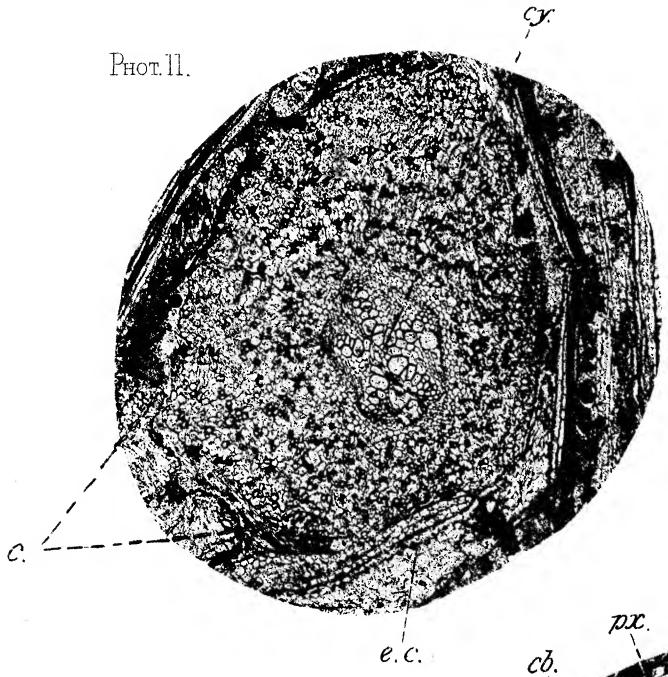


W. Kirman Photo.

Photographs 7–10, Lyginodendron Oldhamium.

Phot. 11.



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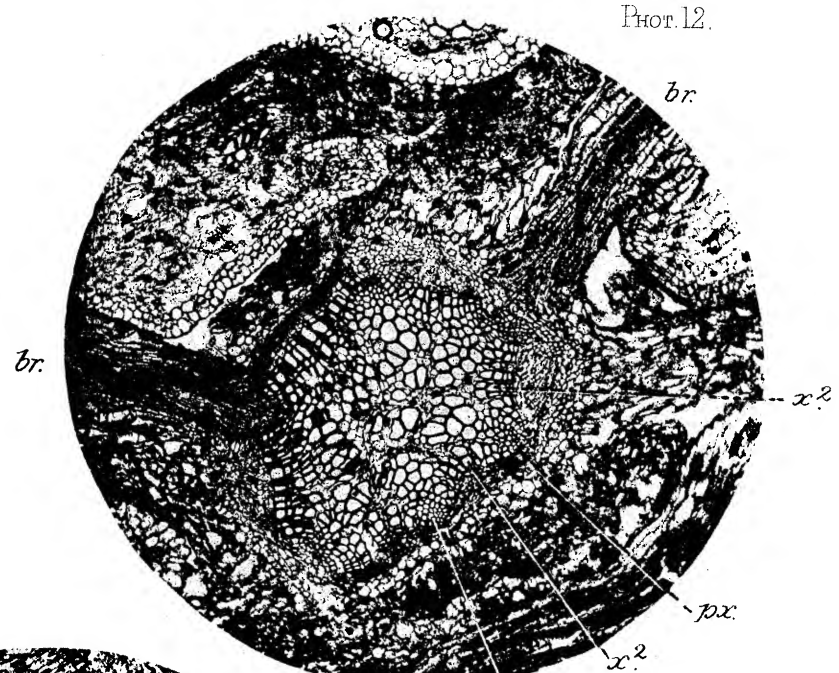

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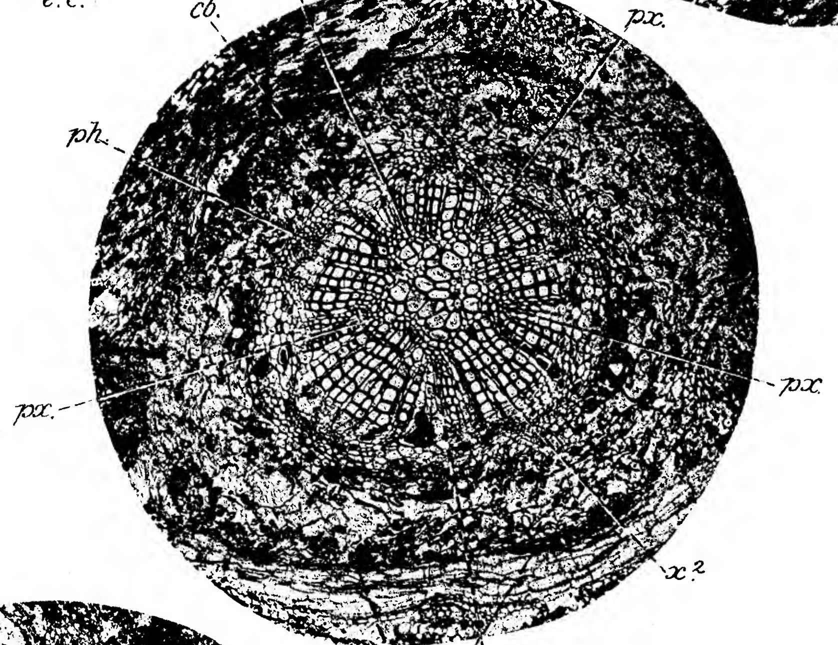

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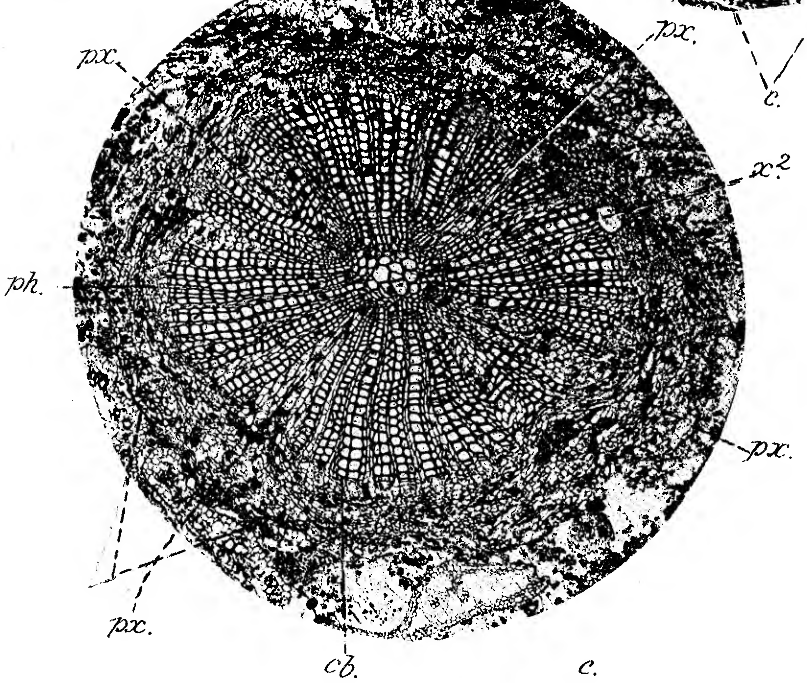

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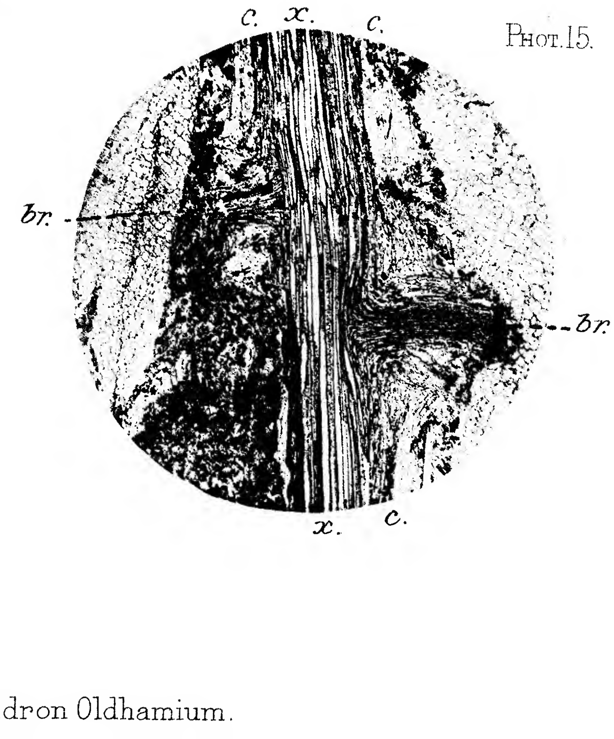

W. Kirman. Photo.

Photographs 11–15. Lyginodendron Oldhamium.

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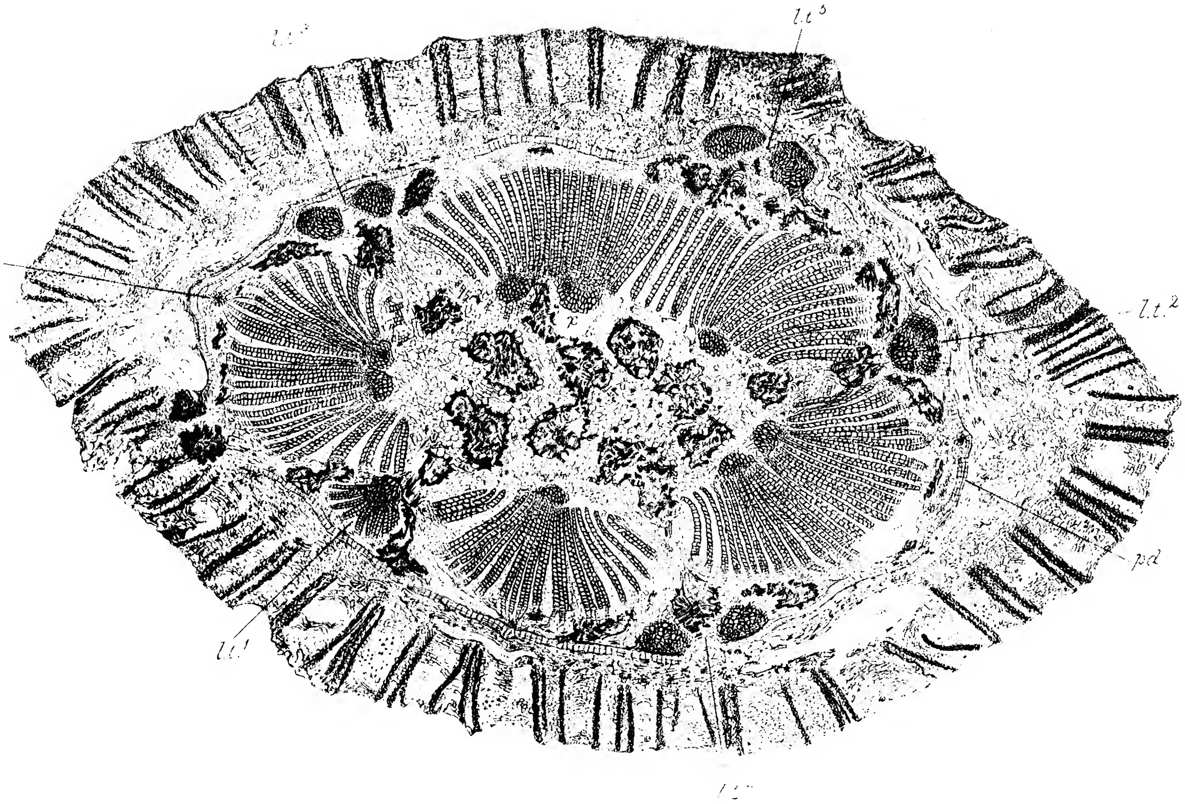

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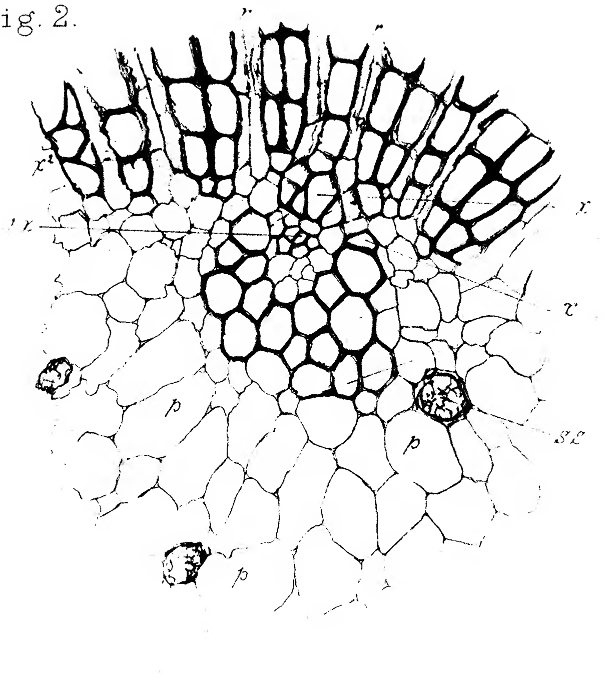
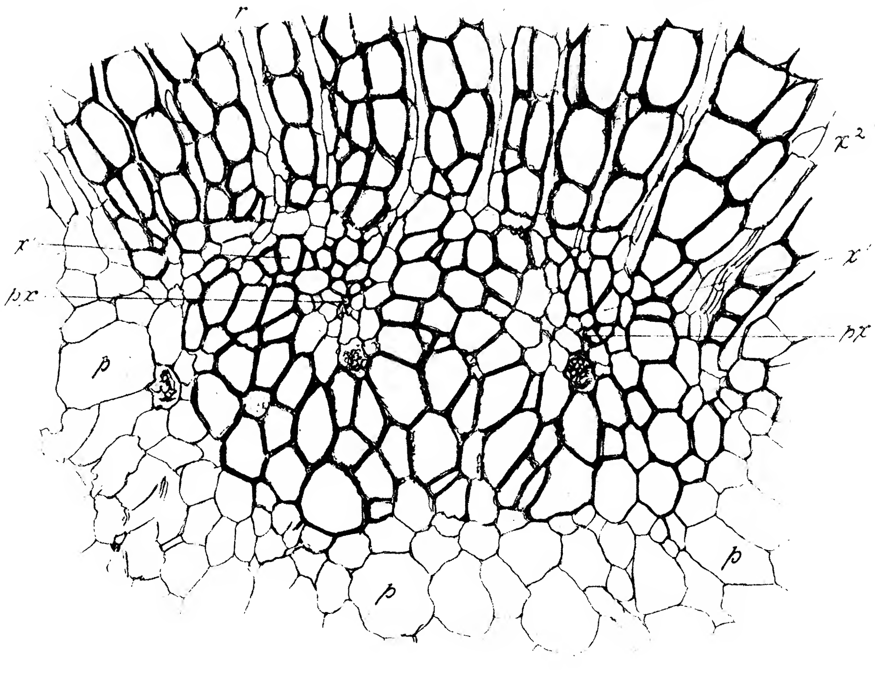


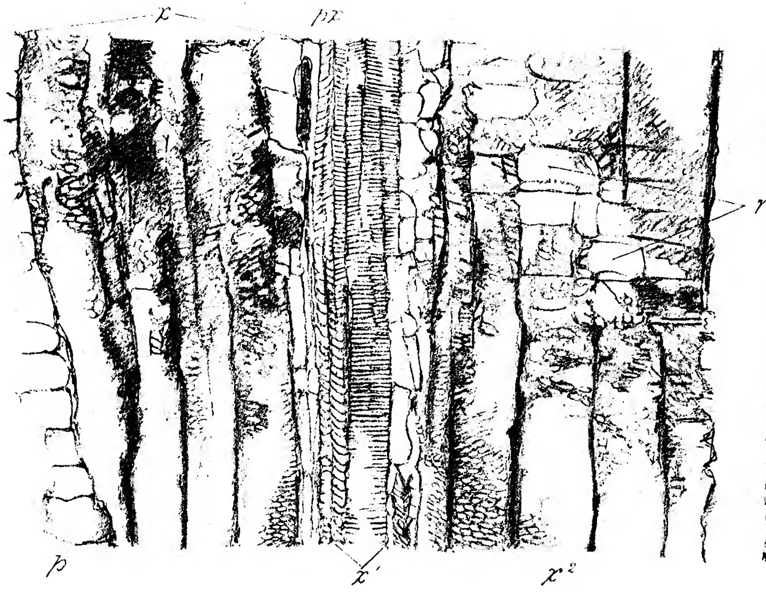
Fig. 3.



Figs. 1–3, Lyginodendron Oldhamium.

G. Brebner del.

Fig. 4.



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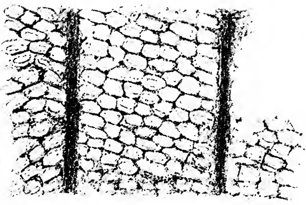


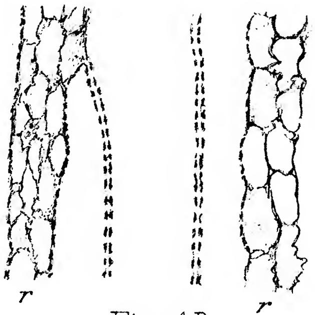
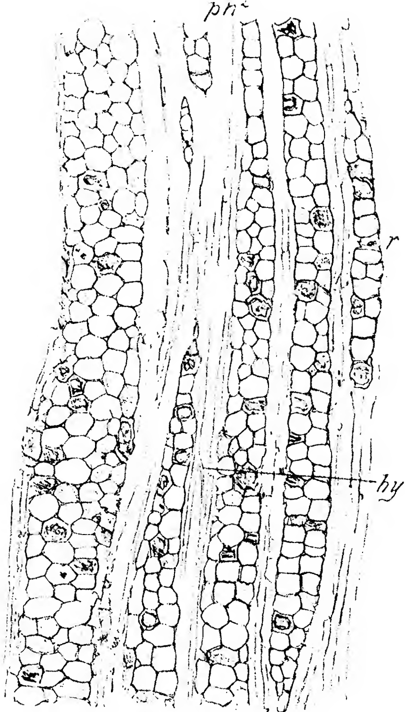


Fig. 4B.

Fig. 7A.



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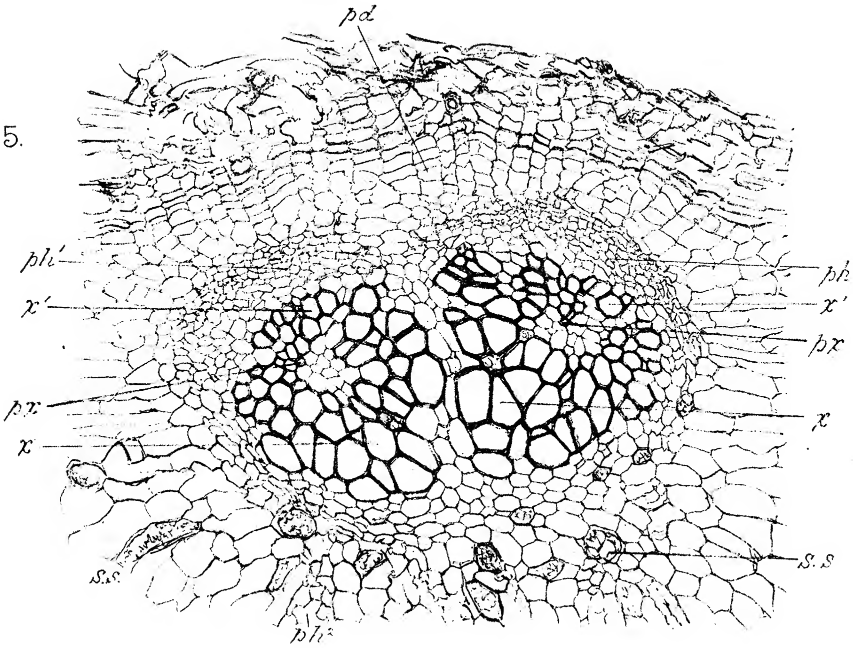

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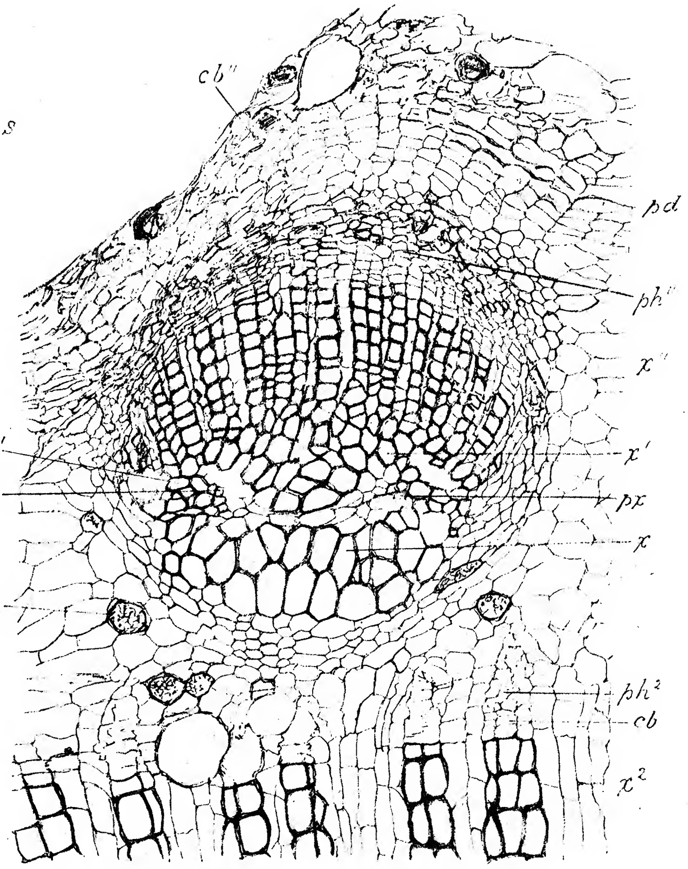
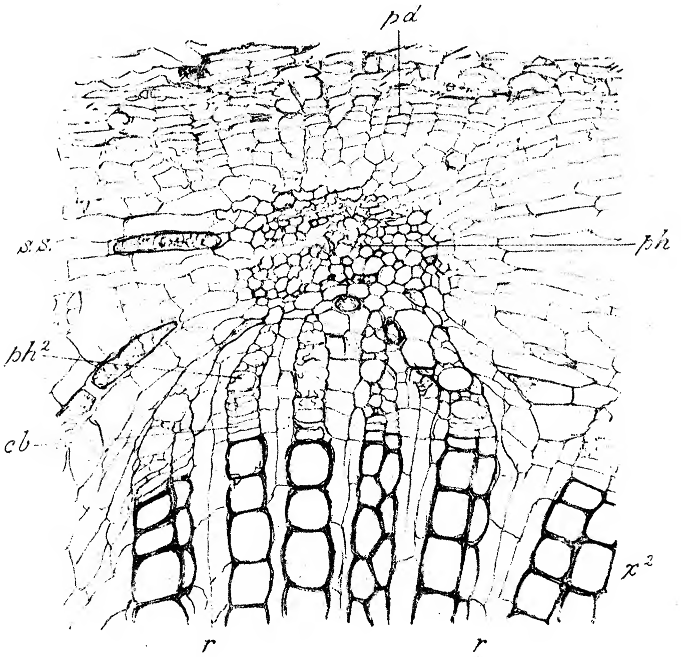


Fig. 7.



Figs. 4–7A Lyginodendron Oldhamium.

G. Brebner del.

Fig. 8.

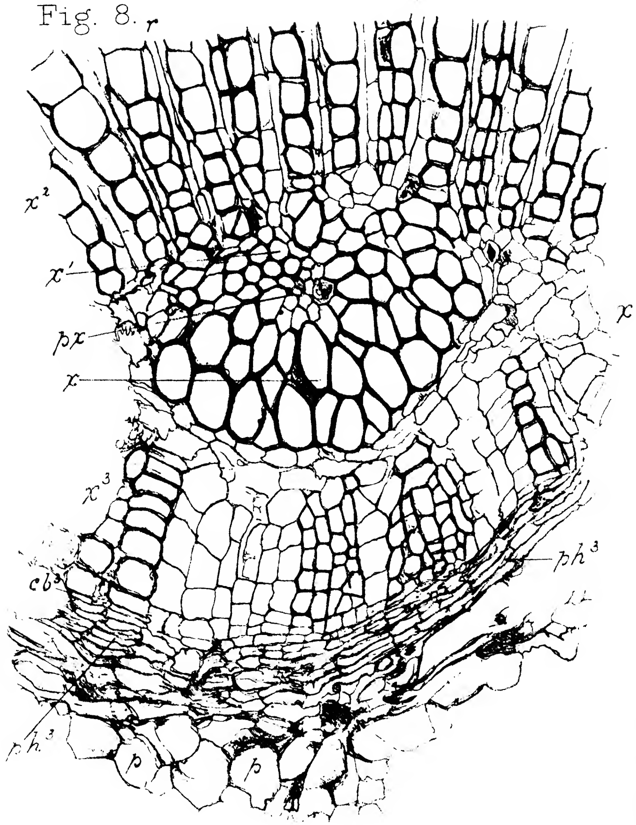
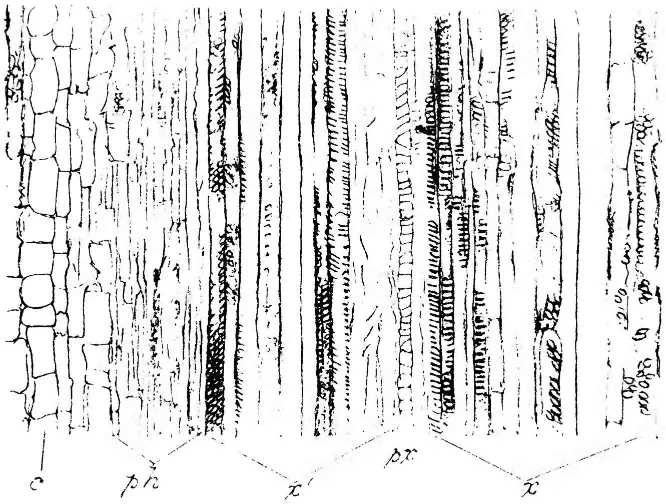


Fig. 13.



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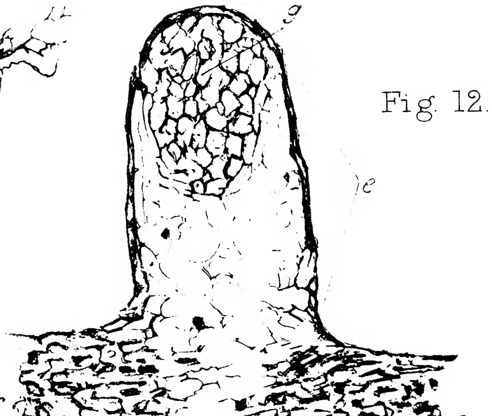

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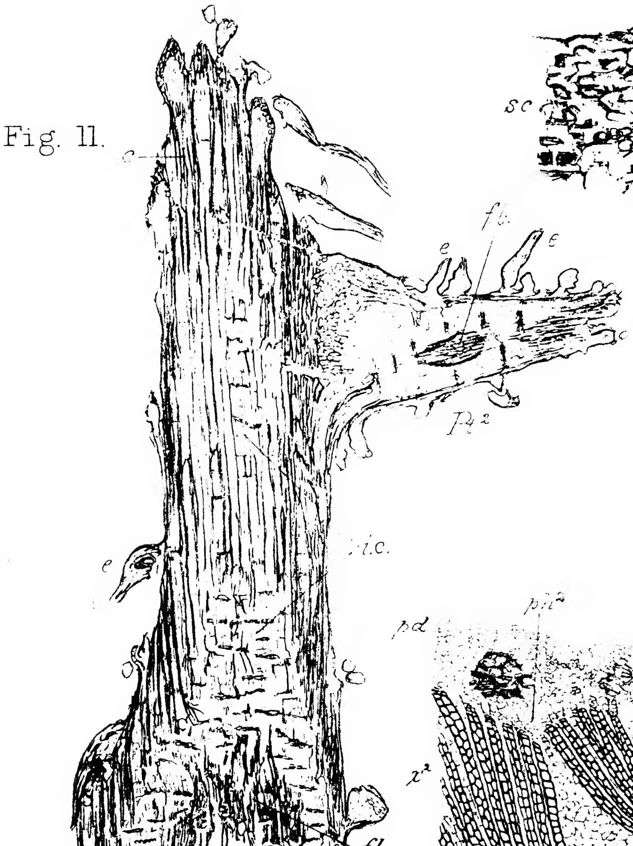

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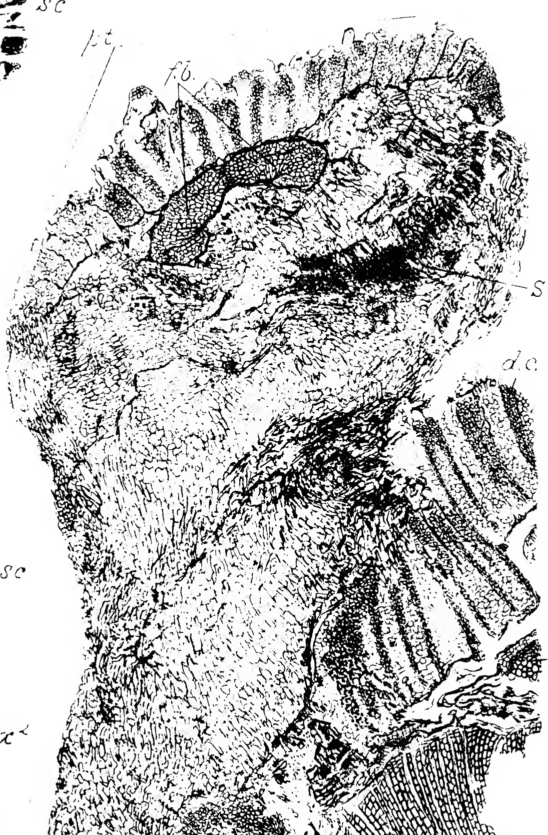

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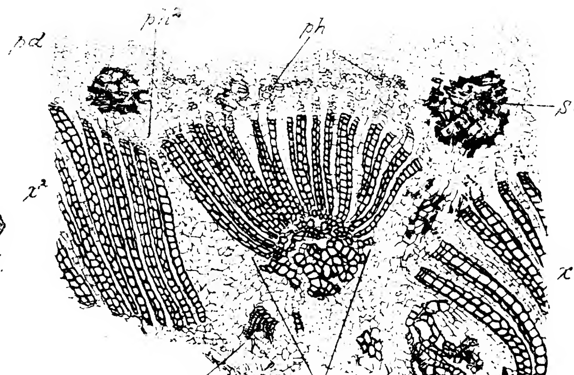
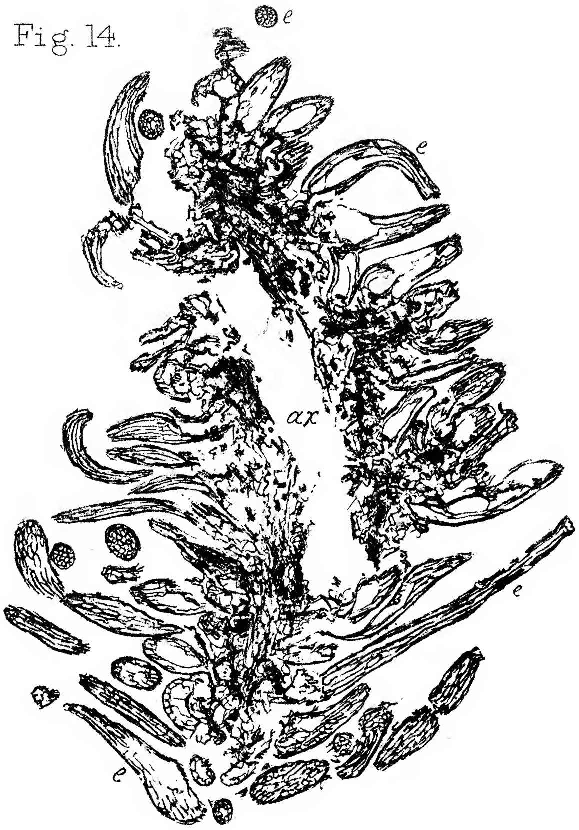


Figs. 8–13, Lyginodendron Oldhamium.

G. Brebner del.

Fig. 14.



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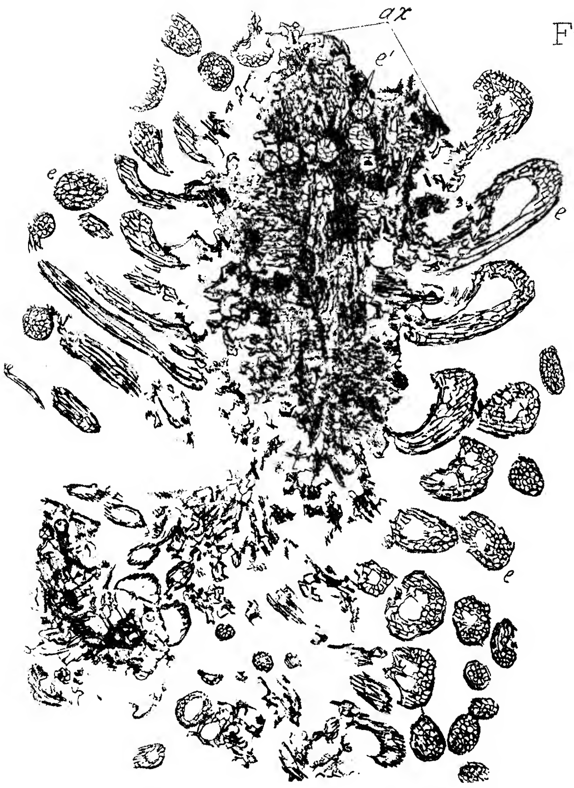


Fig. 16.

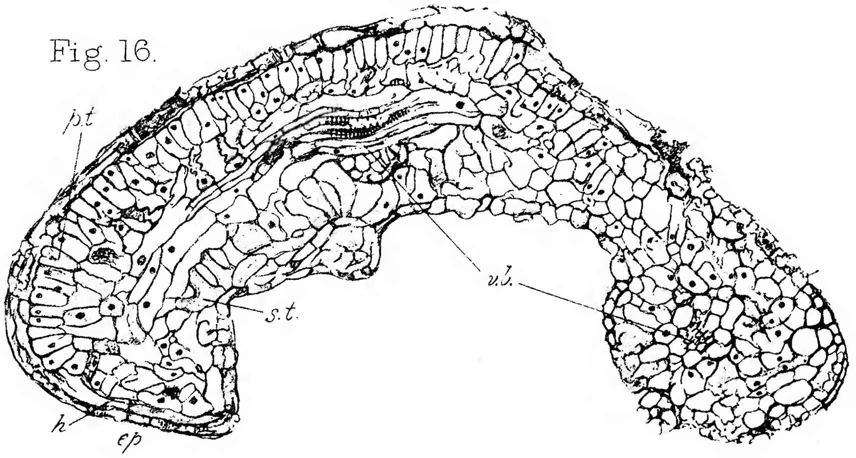


Fig. 17.

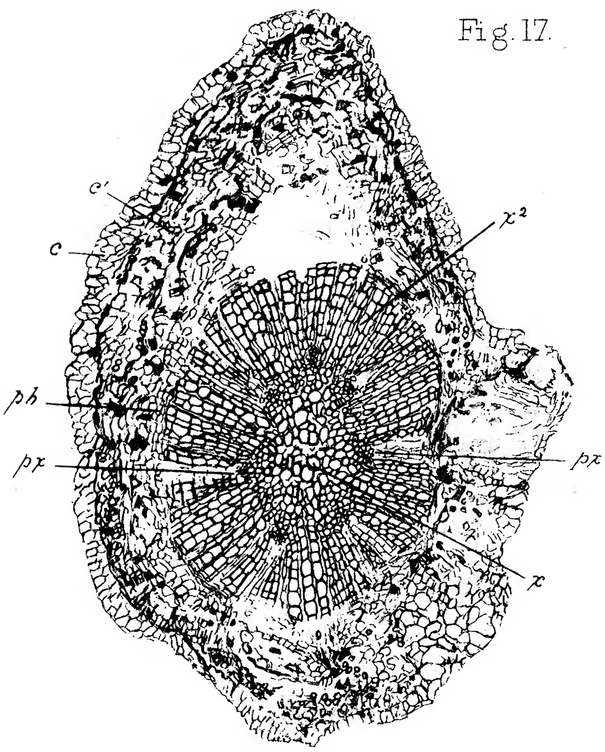
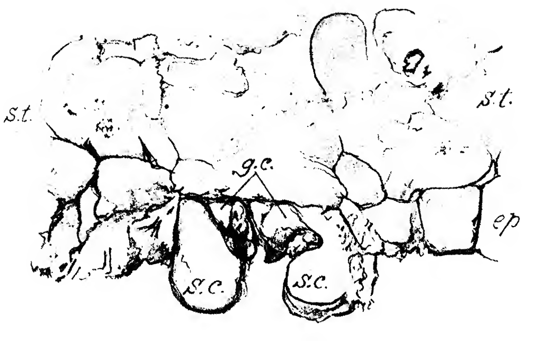


Fig. 16^A.



Figs. 14—17, Lyginodendron Oldhamium.

G. Brebner del.

Fig. 18.

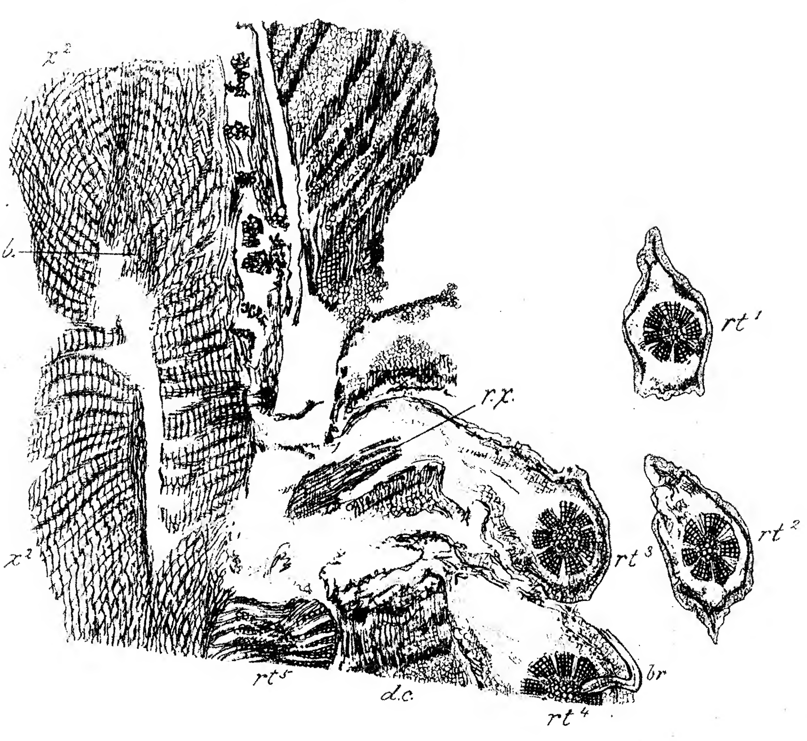
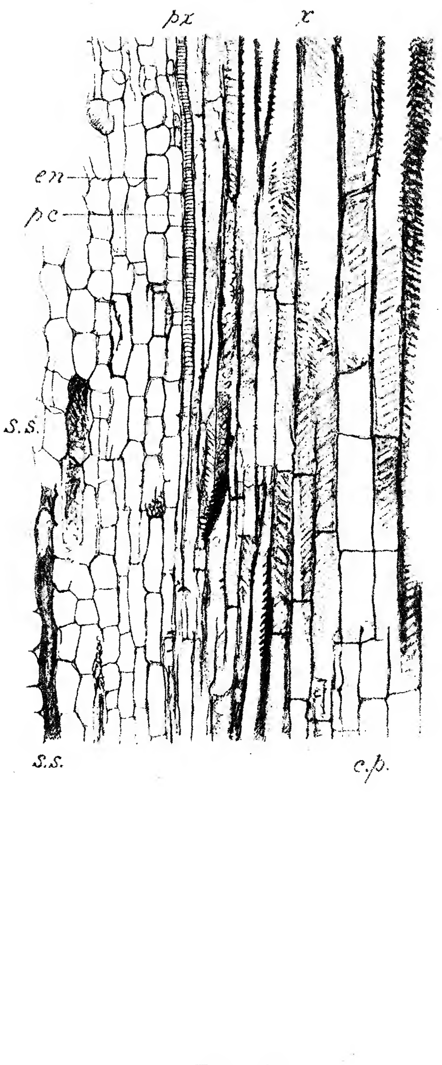


Fig. 19.



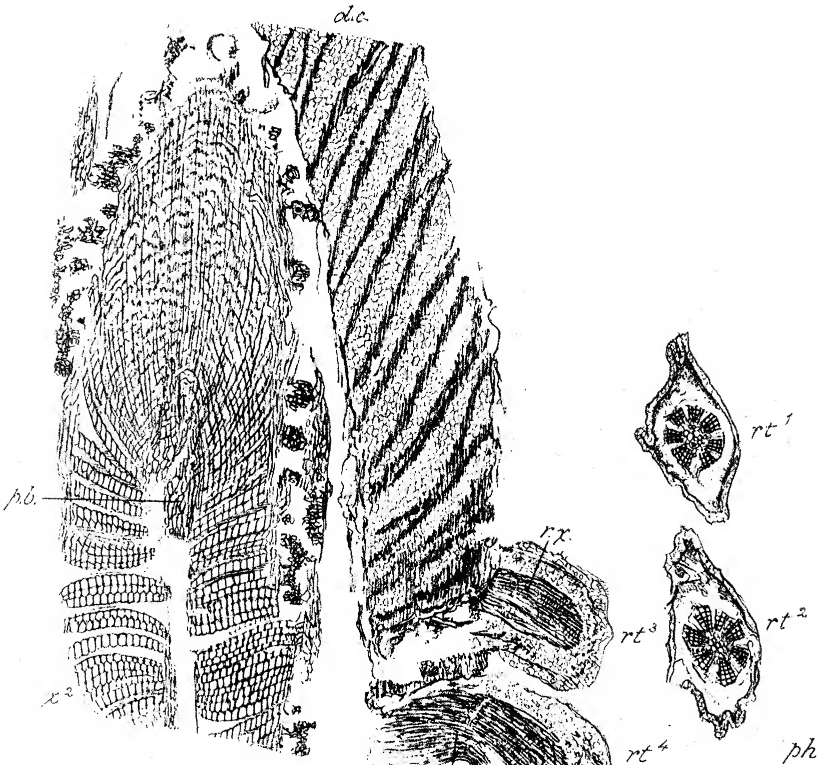
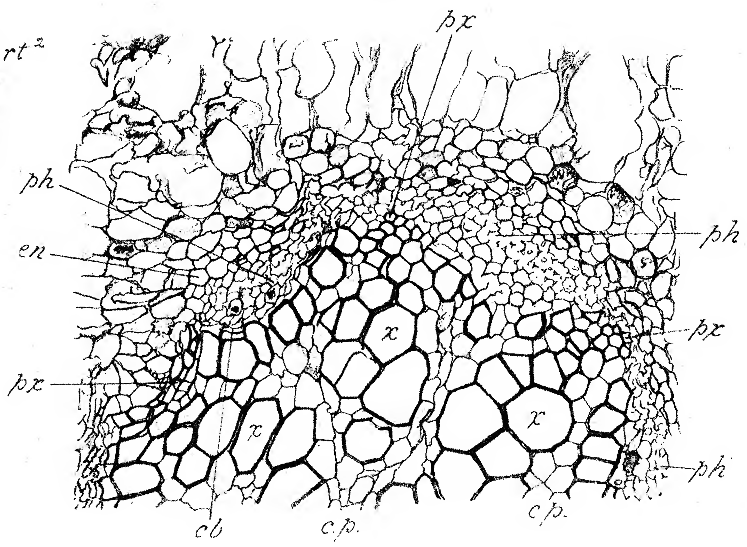


Fig. 18A.

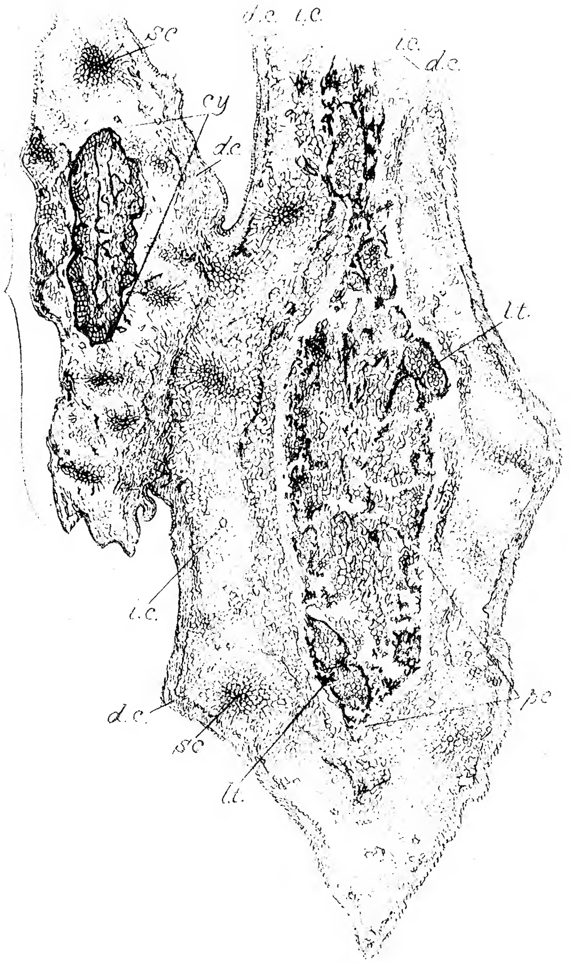
Fig. 20.



Figs. 18.—20, Lyginodendron Oldhamium.

G. Brebner del.

Fig. 21.



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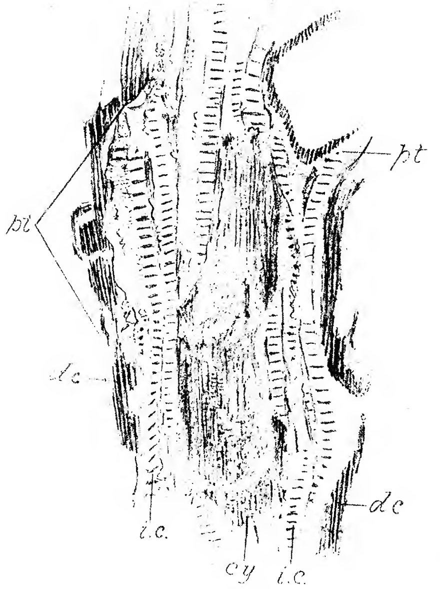

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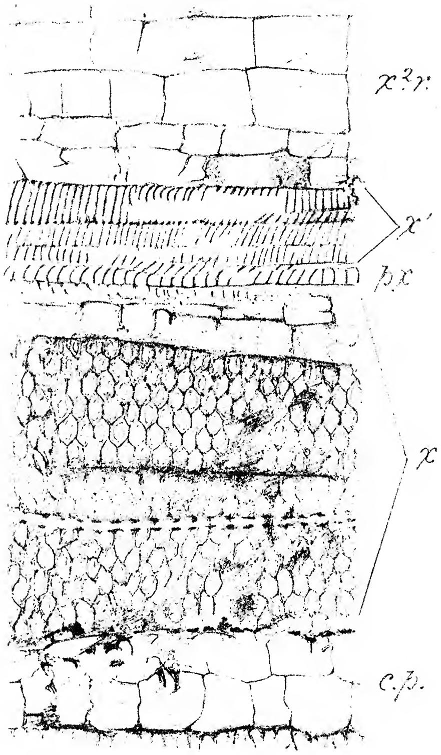

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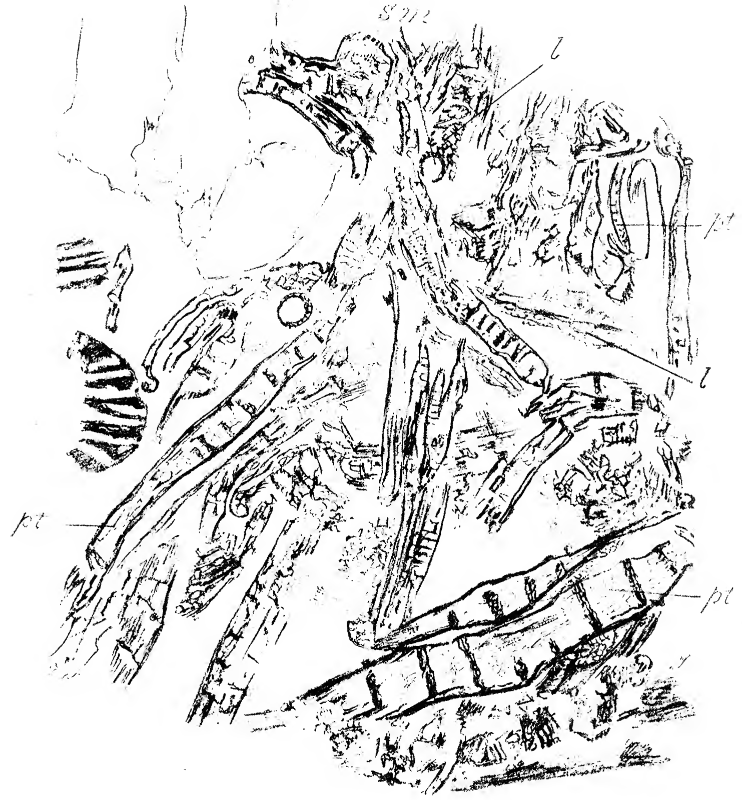

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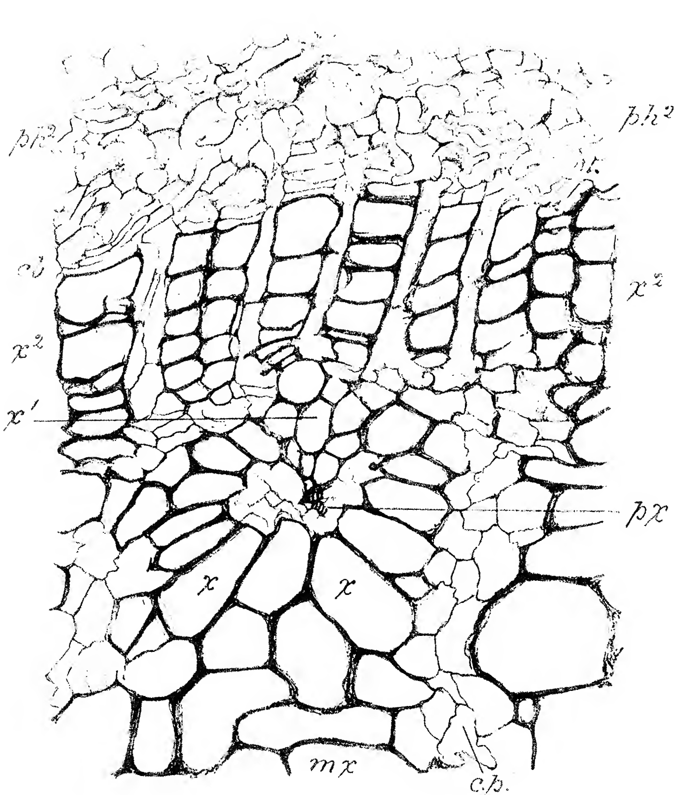


Figs. 21–25, Heterangium Grievii.

G. Brebner del.

Fig. 26.

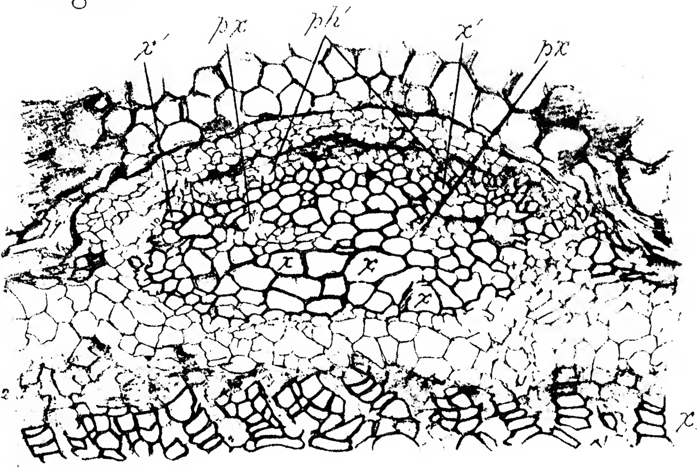


Fig. 27.

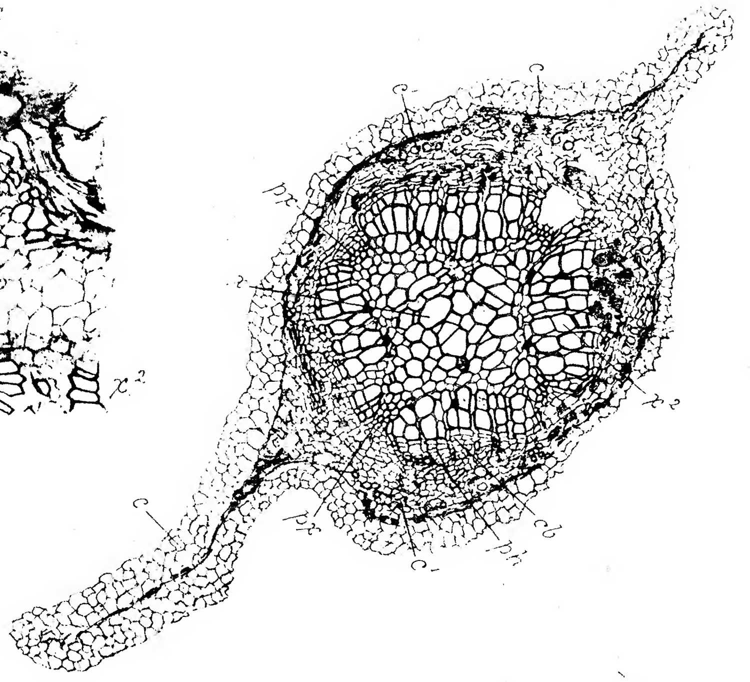


Fig. 29.

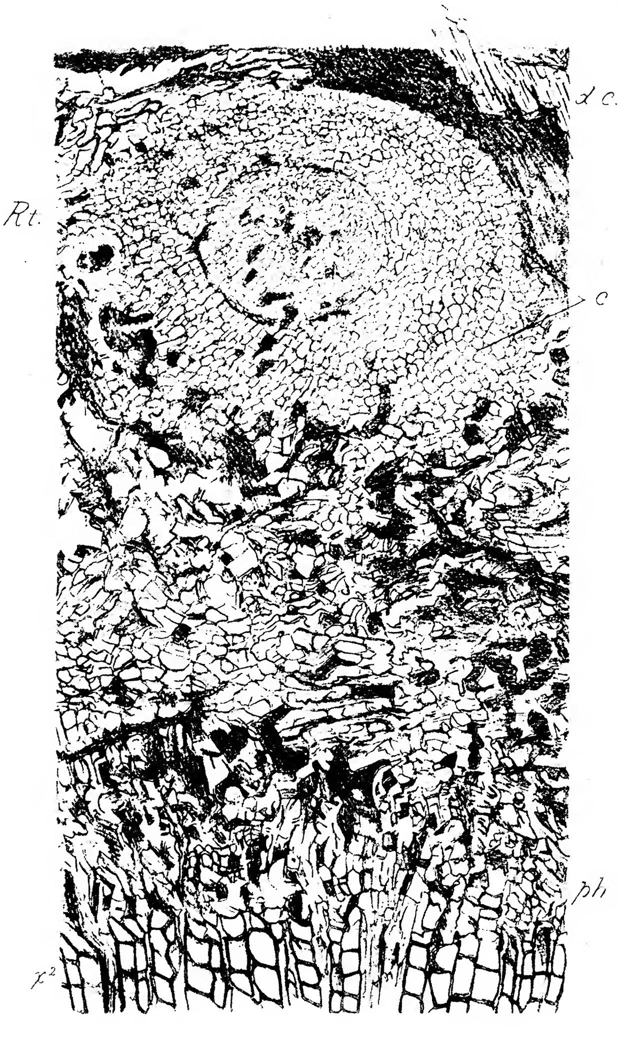
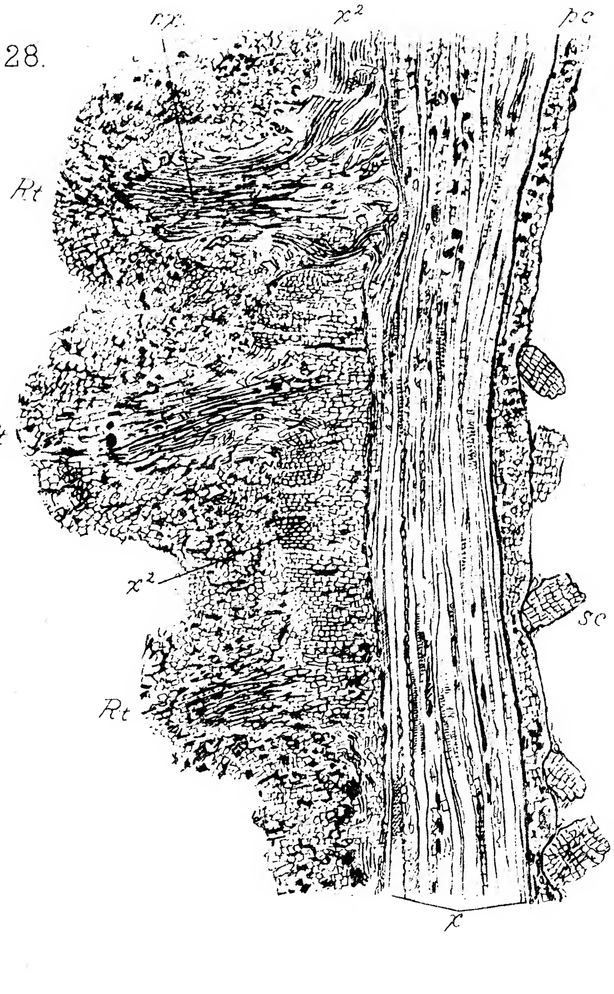


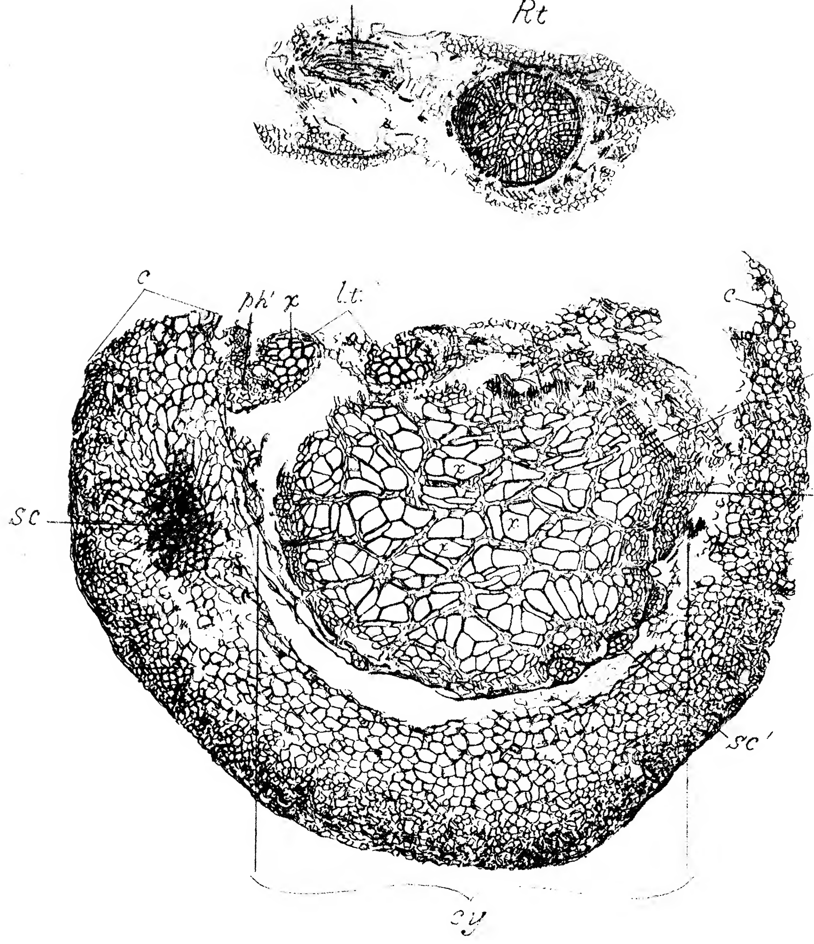
Fig. 28.



Figs. 26–29. Heterangium Grievii.

G. Brebner del.

Fig. 30.



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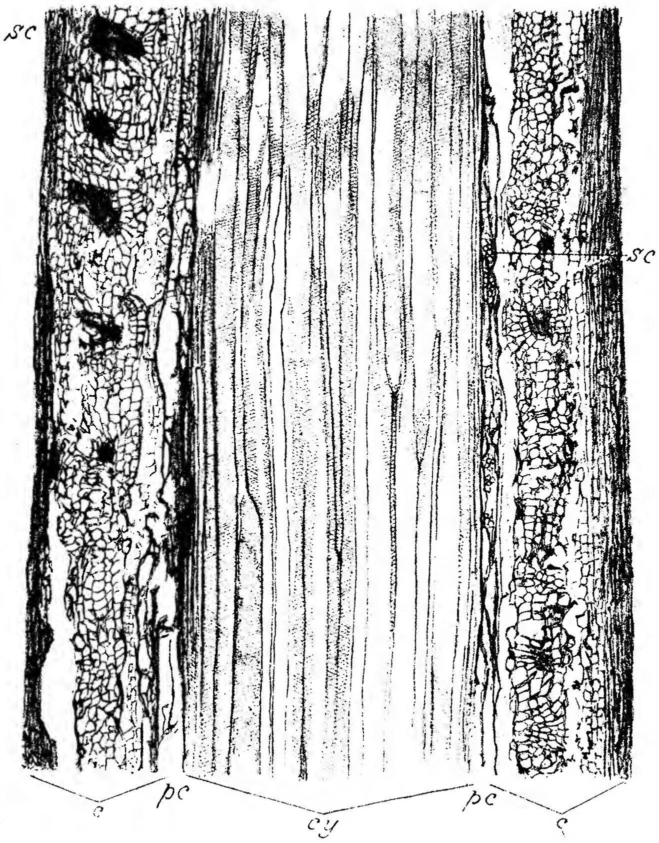


Fig. 32.

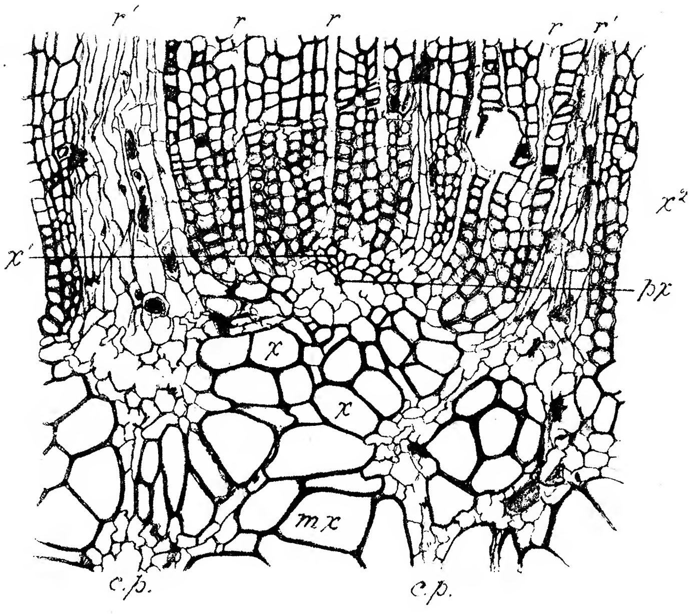
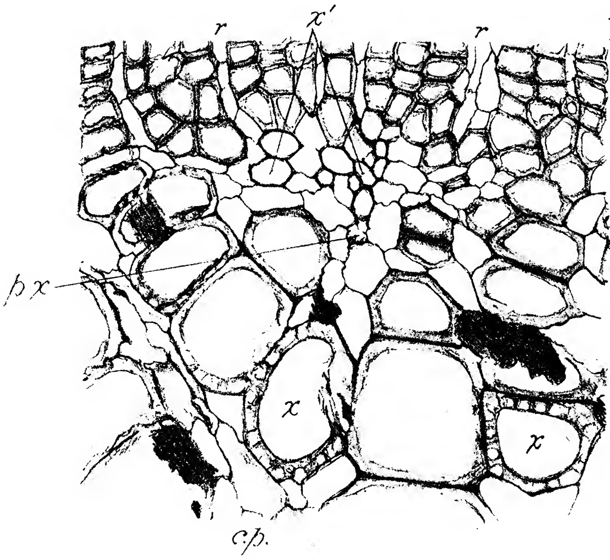


Fig. 33.



Figs. 30 and 31, Heterangium sp.
Figs. 32 and 33, Heterangium tiliæoides.

G. Brebner del.

Fig. 34.

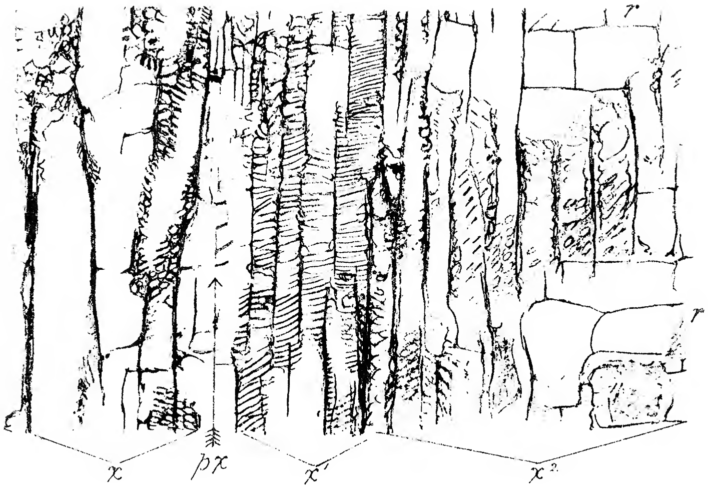


Fig. 35.

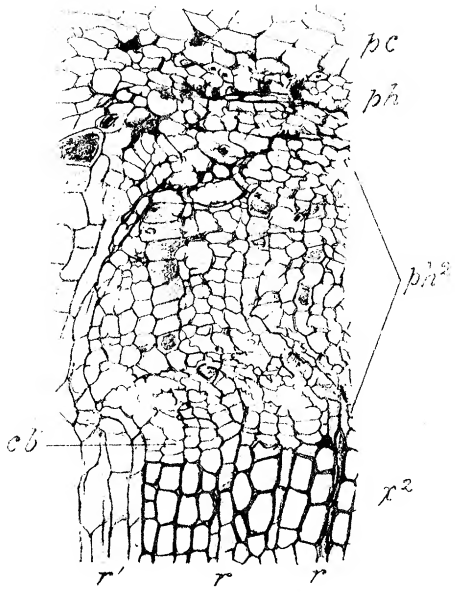


Fig. 36.

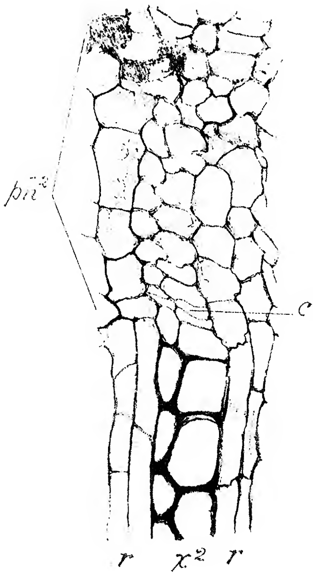


Fig. 37.

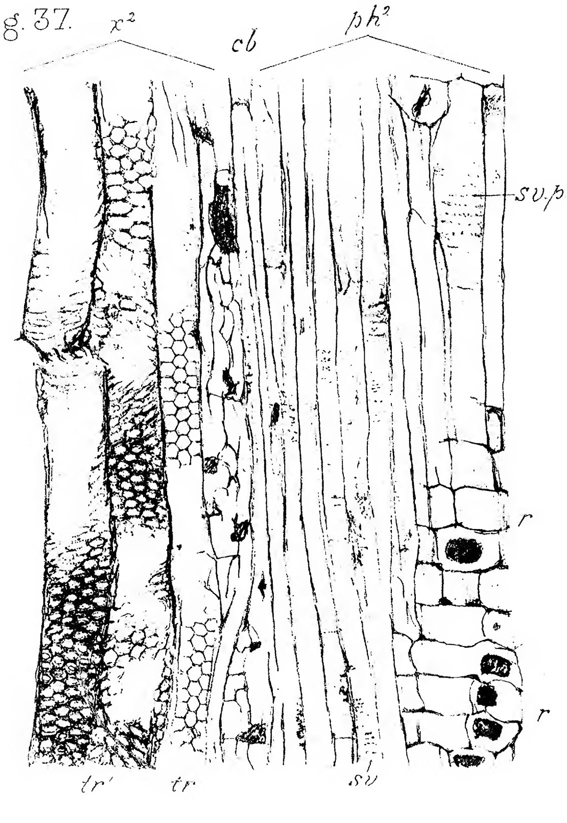


Fig. 38A.

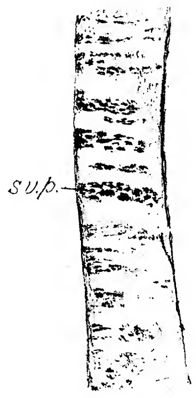
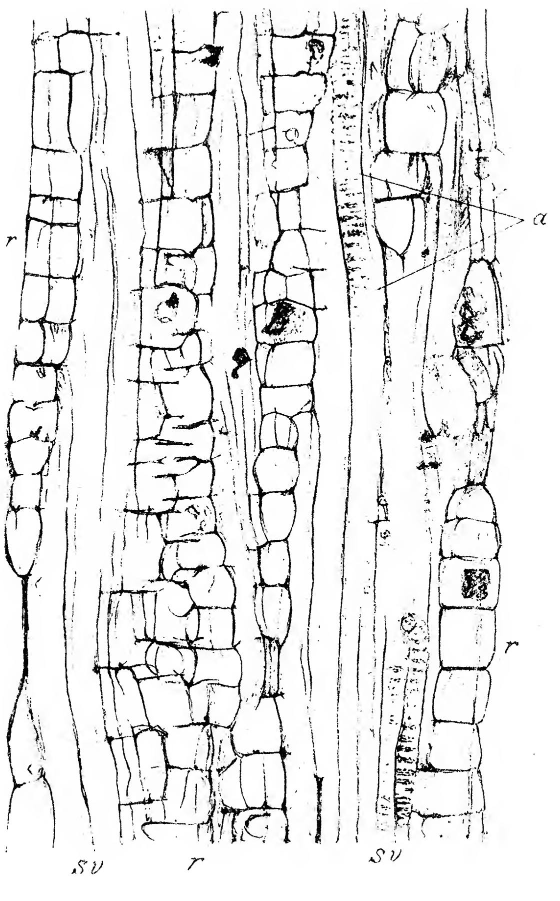


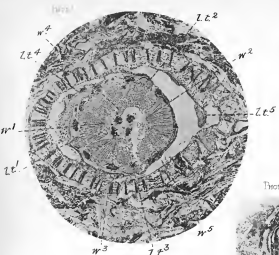
Fig. 38.



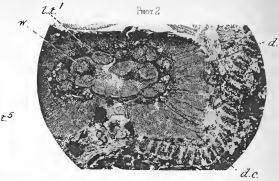
Figs. 34–38A. Heterangium tiliæoides.

G. Brebner del.

PHOT 1



PHOT 2



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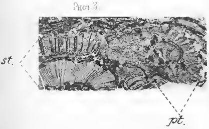
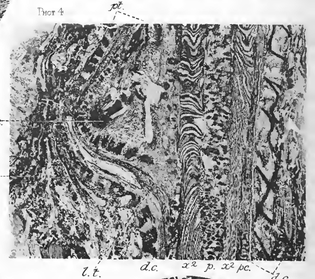
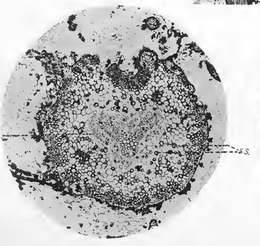


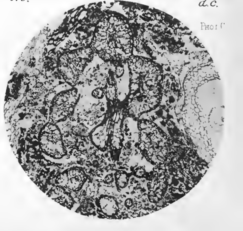
PHOT 4



PHOT 5



PHOT 6



Photographs 1–6. Lyginodendron Oldhamium

PLATE 18.

Photograph 1. Transverse section of a medium-sized stem passing through an internode. The outer, or *Dictyoxylon* cortex is perfect; the inner cortex only remains here and there, especially on the left. $l.t.^1$–$l.t.^5$, the five leaf-traces in the pericyle, numbered in order from within outwards. Note that $l.t.^1$ is a single bundle, the rest more or less double ($l.t.^5$ accidentally displaced); $w.^1$–$w.^5$, the perimedullary xylem-strands alternating with the external bundles; they are numbered according to the leaf-traces on their anodic side. Between *w.* and *l.t.* are the secondary wood and the phloëm. Compare Plate 21, fig. 1, and for details see Plates 21 and 22, figs. 2, 3, 5, 6 and 7. × 6½. C.N. 1640 (see p. 706).

Photograph 2. Transverse section of a young stem at the commencement of secondary growth. *d.c.*, *Dictyoxylon* cortex; $l.t.^1$, the innermost of the four leaf-traces; the remaining three are double; *w.*, one of the six perimedullary strands of xylem. Between *w.* and *l.t.* a thin zone of secondary wood is seen. The external layer of cortex to the right is not evidently connected with this stem. × 11. C.N. 1144D (see pp. 710 and 714).

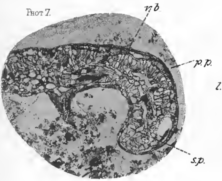
Photograph 3. Part of transverse section of a stem, showing the base of a petiole in connection with it. *st.*, stem; *pt.*, petiole. The petiole contains a double bundle, which is concentric. Plate 19, photograph 8A, and Plate 23, fig. 10 show other sections of the same specimen. × 3. C.N. 1980 (see p. 725).

Photograph 4. Radial section of stem and petiole, showing the connection between them. *d.c.*, *Dictyoxylon* cortex of stem; *pc.*, pericycle; $x.^2$, secondary wood; *p.*, pith; *pt.*, petiole, cut off at this point; *sc.*, axillary sclerotic band; *c.*, outer limit of cortex of petiole; *lt.*, leaf-trace bundle, entering petiole from stem. × 3½. C.N. 1982 (see p. 725).

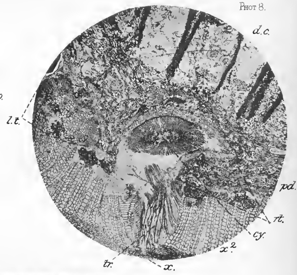
Photograph 5. Transverse section of a small secondary branch of a petiole. The outer cortex has the usual *Dictyoxylon* structure; *s.s.*, secretory sacs of the inner cortex; *v.b.*, the concentric vascular bundle with V-shaped xylem completely surrounded by phloëm. × about 35. C.N. 145 (see p. 728).

Photograph 6. Transverse section of part of the lamina, cut through a number of leaflets just separating from one another. A part of one of the leaflets is displaced and seen in obliquely superficial view. × about 35. C.N. 1885D (see p. 727).

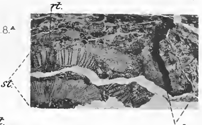
PHOT 7.



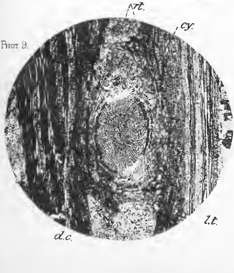
PHOT 8.



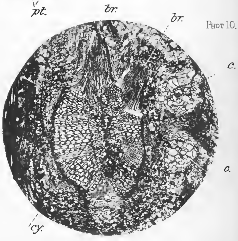
PHOT 8.ᴬ



PHOT 9.



PHOT 10.



Photographs 7–10. Lyginodendron Oldhamium.

PLATE 19.

Photograph 7. Vertical section of a leaflet. *p.p.*, palisade parenchyma; above this is the hypoderma, and then the epidermis; *s.p.*, spongy parenchyma; *v.b.*, vascular bundle, in obliquely longitudinal section. On the under side of the leaf is an outgrowth, perhaps of the same nature as the cortical emergences. × about 70. C.N. 1196 (see p. 730).

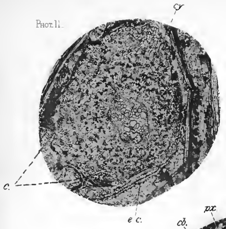
Photograph 8. Part of a transverse section of a large stem, passing through the base of an adventitious root. *rt.*, outer limit of cortex of root; *cy.*, central cylinder of root, which has formed secondary wood; *tr.*, tracheides connecting the base of the root with the wood of the stem; *x.*, remains of primary wood of stem; *x.*², its secondary wood; *pd.*, periderm; *d.c.*, *Dictyoxylon* cortex; *l.t.*, large leaf-trace bundle. × about 12. C.N. 1144B (see p. 733).

Photograph 8A. Another section of the same specimen as photograph 3, taken higher up. *st.*, stem; *pt.*, petiole. Note the dark axillary band at the junction of the two. At *rt.* a root is seen in longitudinal section, passing out from the wood through the cortex. × 3. C.N. 1981 (see pp. 725 and 734).

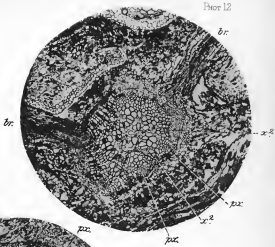
Photograph 9. Part of tangential section of the cortex of a large stem, showing base of adventitious root; *l.t.*, leaf-trace bundle of stem; *d.c.*, part of the *Dictyoxylon* cortex; *rt.*, outer limit of cortex of root; *cy.*, its central cylinder, with abundant secondary wood. × about 15. C.N. 1883 (see p. 734).

Photograph 10. Another root from the same preparation; it has just become free from the stem, part of the cortex of which is seen at *d.c.* c., c., cortex of root; *cy.*, middle of its central cylinder; *br.*, *br.*, two rootlets arising from the root. × 28. C.N. 1885 (see p. 734).

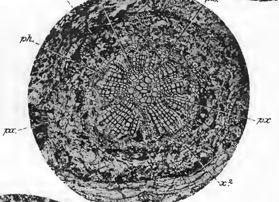
Phot 11



Phot 12



Phot 13



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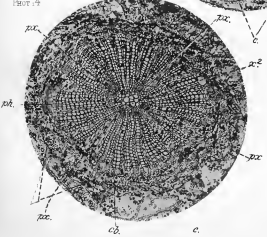
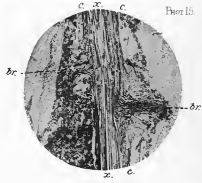


Phot 15



Photographs 11–15. Lyginodendron Oldhamium

PLATE 20.

Photograph 11. Transverse section of a young root, before secondary growth has begun. *c.*, cortex of root; *e.c.*, external cortical layer; *cy.*, the pentarch stele, in which the alternating xylem and phloëm-strands are seen. The cortex is full of secretory sacs. × about 30. C.N. 1634 (see p. 736).

Photograph 12. Transverse section of a root branching. *br.*, *br.*, two rootlets, arising opposite two of the protoxylem-groups, of which there are six in all, two being lettered *px.*; $x.^2$, secondary wood, beginning to form between the protoxylem-groups. × about 30. C.N. 1899 (see pp. 738 and 740).

Photograph 13. Transverse section of a pentarch root, with secondary thickening. *px.*, the five protoxylem-groups, to each of which a ray corresponds; *ph.*, a phloëm-group; $x.^2$, secondary wood; *cb.*, cambium; *c.*, outer limit of cortex. × about 30. C.N. 1631 (see p. 739).

Photograph 14. Transverse section of a very advanced tetrarch root. *px.*, the four protoxylem-groups; *ph.*, a phloëm-group, in which the primary phloëm is very distinct; $x.^2$, secondary wood; *cb.*, cambium; *c.*, outer limits of cortex. × about 20. C.N. 1632 (see p. 739).

Photograph 15. Longitudinal median section of a root, giving off two rootlets. *br.*, *br.*, the two rootlets; *c.*, cortex of main root; *x.*, xylem of its stele. × about 12. C.N. 1899A (see p. 740).

Fig 1

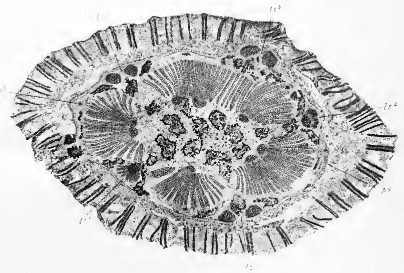


Fig 2.

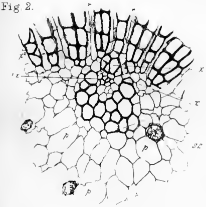
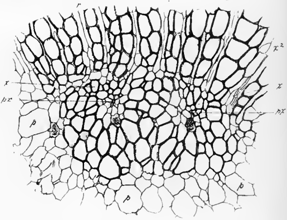


Fig. 3.



Figs 1-3. Lyginodendron Oldhamium.

PLATE 21.

Fig. 1. Transverse section of a very well-preserved stem. The *Dictyoxylon* cortex shows dilatation conspicuously. Next comes the inner cortex. *pd.*, periderm, at outer limit of pericycle; $lt.^1$–$lt.^5$, five leaf-traces passing through the pericycle, numbered in order from within outwards; their arrangement corresponds to a $\frac{2}{5}$ phyllotaxis; *ph.*, one of the primary phloëm-groups; secondary phloëm and cambium shown; within these is the wide secondary wood; *x.*, one of the eight perimedullary xylem-strands; pith and pericycle contain numerous sclerotic groups. × 6. From a new specimen (in the possession of D. H. Scott), obtained through Professor Bower, F.R.S., from Oldham (see pp. 706 and 708).

Fig. 2. Part of transverse section from the same specimen as Plate 18, photograph 1, showing the xylem-strand marked $w.^2$ in that photograph. The mesarch structure is evident. *px.*, protoxylem; *x.*, centripetal portion of primary wood; $x.^1$, centrifugal portion of the same; $x.^2$, part of secondary wood; *r.*, *r.*, rays; *p.*, *p.*, pith; *s.s.*, secretory sac. × 100. C.N. 1884 (see pp. 709 and 712).

Fig. 3. Another section from the same specimen, showing the large double xylem-strand, marked $w.^5$ in photograph 1. Lettering as in fig. 2. × 100. C.N. 1640 (see pp. 709, 711, and 712). (C.N. 1640 and 1884 are adjacent and practically identical sections from the same stem.)

Fig. 4.

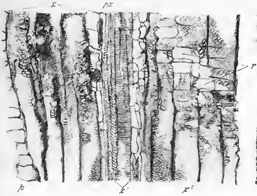
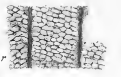


Fig. 4A.



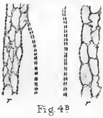


Fig. 4B

Fig 7A.

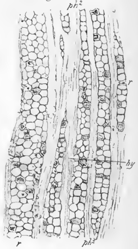


Fig. 5.

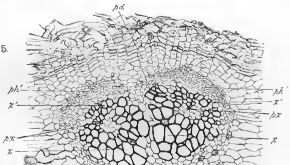


Fig. 6.

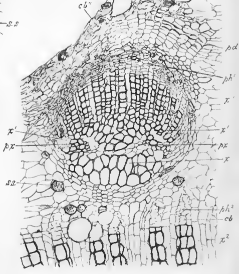
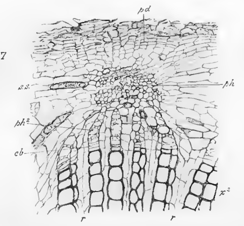


Fig 7



Figs. 4–7A Lyginodendron Oldhamium.

PLATE 22.

Fig. 4. Part of a radial section, passing through one of the primary xylem-strands, and showing mesarch structure. Lettering as in figs. 2 and 3. × 100. C.N. 1982 (see p. 712).

Fig. 4A. Parts of secondary tracheides from same section, to show bordered pits. × 150.

Fig. 4B. Ditto in tangential section. *r.*, secondary rays. × 150. C.N. 1985 (see p. 716).

Fig. 5. Part of transverse section showing the leaf-trace bundle, marked *l.t.*¹ in photograph 1, illustrating the collateral mesarch structure. *px.*, *px.*, the two protoxylem-groups of the bundle; *x.*, centripetal part, *x.'*, centrifugal part, of its primary wood; *x.''*, secondary wood of bundle; *cb.''*, its cambium; *ph.''*, its phloëm; *x.*², secondary wood of the stem; *cb.*, cambium; *ph.*², phloëm; *s.s.*, secretory sacs; *pd.*, periderm, at outside of pericycle. × 70. C.N. 1640 (see pp. 709 and 712).

Fig. 6. Transverse section through the leaf-trace bundle, *l.t.*², of photograph 1. At this level the bundle has become double, and is without secondary tissues. The structure is exactly that of foliar bundles in Cycadeæ, *e.g.*, *Stangeria*. Lettering as in fig. 5. × 70. C.N. 1884 (see pp. 709 and 713).

Fig. 7. Part of transverse section from the same specimen, to show cambium and phloëm. *x.*², secondary wood; *r.*, *r.*, rays; *cb.*, cambium; *ph.*², secondary phloëm; *ph.*, primary phloëm; *s.s.*, secretory sacs in pericycle; *pd.*, periderm. × 70. C.N. 1640 (see p. 715).

Fig. 7A. Part of a tangential section through the secondary phloëm. *ph.*², strands of sieve-tubes and elongated parenchyma; *r.*, *r.*, phloëm-rays; *hy.*, branched fungal hypha. × 70. From one of the new Oldham specimens (D. H. S.) (see p. 716).

Fig. 8

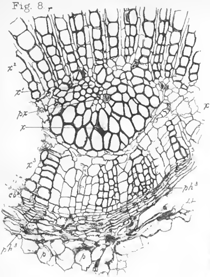


Fig 13

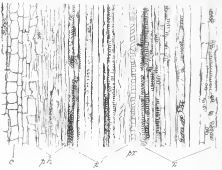


Fig 12

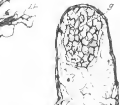


Fig. 11.

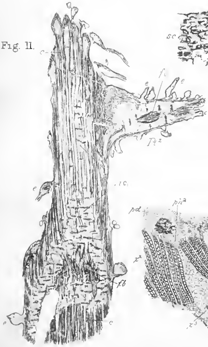


Fig 10

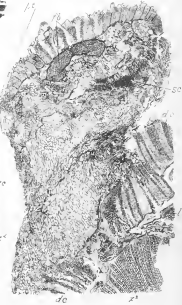
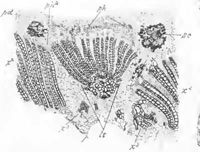


Fig. 9.



Figs. 8–13, Lyginodendron Oldhamium.

PLATE 23.

Fig. 8. Part of a transverse section to show anomalous secondary tissues in the pith, x^2., normal secondary wood; *r.*, *r.*, rays; *px.*, protoxylem of normal primary xylem; *x.*, centripetal, *x.'*, centrifugal, part of primary xylem; $x.^3$, anomalous medullary wood; $cb.^3$, anomalous cambium; $ph.^3$, anomalous phloëm; *p.*, *p.*, pith. × 70. C.N. 1190 (see p. 722).

Fig. 9. Part of a transverse section, to show a leaf-trace bundle in the intermediate position between pith and pericycle. *lt.*, leaf-trace, with a large fan of secondary tissue; *ph.*, phloëm of the leaf-trace, continuous on the left with the phloëm-zone ($ph.^2$) of the stem; $x.^2$, secondary wood of stem; $x.^3$, $x.^3$, patches of anomalous wood in trace-gap; *p.*, *p.*, pith; *pd.*, periderm. × 14. From one of the new Oldham specimens (D. H. S.). (see p. 710).

Fig. 10. Part of a transverse section, to show petiole in connection with the stem. From the same series as photographs 3 and 8A, and intermediate between them. *pt.*, petiole; *f.b.*, its double bundle; *sc.b.*, sclerotic axillary band (*cf.* photograph 4); *d.c.*, Dictyoxylon cortex of stem; *lt.*, part of a leaf-trace bundle; x^2., secondary wood. × 7. Slide 56 (D. H. S.) (see p. 725).

Fig. 11. Obliquely longitudinal section of the *same petiole*, when it has become free from the stem. $pt.^2$, branch of the petiole; *f.b.*, *f.b.*, vascular bundles of main and branch petioles; *c.*, outer cortex; *i.c.*, inner cortex; *e.*, *e.*, cortical emergences. × 6⅓. C.N. 1979 (see p. 725).

Fig. 12. Part of outer cortex of a petiole, to show an apparently glandular emergence. *sc.*, sclerenchyma of cortex; *e.*, emergence; *g.*, supposed glandular tissue. × 100. C.N. 139 (see p. 730).

Fig. 13. Part of a longitudinal section of a petiole, passing through the bundle, of which about half is shown. *px.*, protoxylem; *x.*, centripetal, *x.'*, centrifugal, part of xylem; *ph.*, phloëm; *c.*, cortical tissue. × 70. C.N. 1985 (see p. 728).

Fig 14.

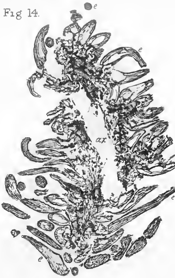


Fig. 15.

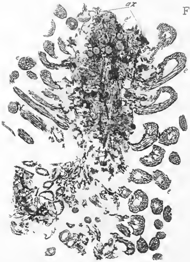


Fig 16

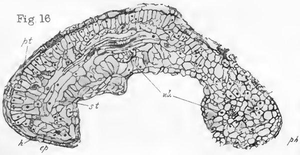


Fig. 17

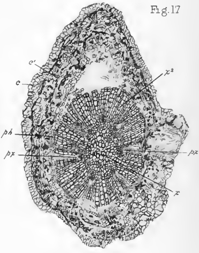
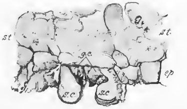


Fig. 16A.



Figs 14—17, Lyginodendron Oldhamium.

PLATE 24.

Fig. 14. Radial section through a bud-like structure. *ax.*, hollow axis of the whole structure; *e.*, *e.*, outgrowths, resembling the cortical emergences of *Lyginodendron.* × 20. C.N. 1859 (see p. 732).

Fig. 15. Tangential section of the same. *e.'*, bases of the outgrowths. × 20. C.N. 1858.

Fig. 16. Leaflet in vertical section. *ep.*, epidermis; *h.*, hypoderma; *p.t.*, palisade tissue; *s.t.*, spongy tissue; *v.b.*, vascular bundles, the one in transverse, the other in longitudinal, section. × 100. C.N. 1197 (see p. 730).

Fig. 16A. From a section of another leaflet, to show a stoma on the lower surface. *s.t.*, part of the spongy tissue; *ep.*, epidermis; *s.c.*, prominent subsidiary cells; *g.c.*, depressed guard-cells of the stoma. × 500. C.N. 1197 (see p. 731).

Fig. 17. Transverse section of *the same root*, *rt.*^{3}, which in figs. 18 and 18A is seen in connection with a stem of *Lyginodendron*. This is from a third section of the specimen, where this root has become free. Note its typical *Kaloxylon* structure. *px.*, *px.*, two of the seven protoxylem-groups; *x.*, primary wood; *x.*^{2}, secondary wood; *ph.*, phloëm; *c.'*, inner cortex; *c.*, outer cortex, or epidermal layer. × 30. C.N. 1885B (see p. 734).

Fig. 18

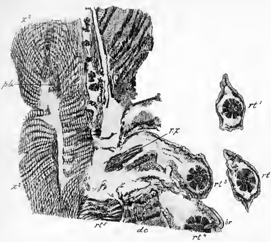
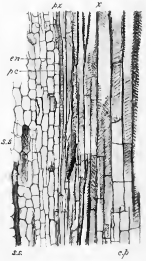


Fig. 19.



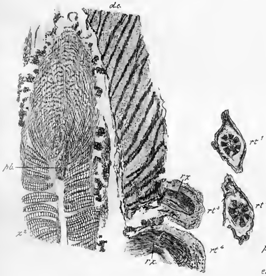
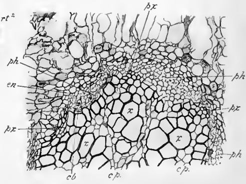


Fig. 18A

Fig 20.



Figs 18.—20, Lyginodendron Oldhamium.

PLATE 25.

Fig. 18. Oblique section of a stem of *Lyginodendron*, showing roots (= *Kaloxylon Hookeri*) in connection with it. $rt.^1$ and $rt.^2$, two free roots; $rt.^3$ and $rt.^4$, two roots in connection with the stem; *r.x.*, part of xylem of $rt.^3$, traversing cortex of stem; *br.*, rootlet given off by $rt.^4$; $rt.^5$, base of a fifth root, at its junction with wood of stem; *d.c.*, *Dictyoxylon* cortex of stem; $x.^2$, its secondary wood; *p.b.*, primary xylem-strands. *Cf.* fig. 17. × 6. C.N. 1885A (see p. 734).

Fig. 18A. Another section of the same specimen. All the four roots, $rt.^1$–$rt.^4$, are shown; $rt.^1$ and $rt.^2$ remain free, $rt.^3$ and $rt.^4$ are here seen in obliquely longitudinal section; *r.x.*, xylem of roots; that of $rt.^4$ can be traced through cortex of stem. Lettering as before. × 6. C.N. 1885C (see p. 734).

Fig. 19. Part of a radial section of a root, to show position of protoxylem. *px.*, protoxylem; *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *pc.*, *en.*, probable pericycle and endodermis; *s.s.*, secretory sacs in cortex. × 100. C.N. 1633 (see p. 736).

Fig. 20. Part of a transverse section of a hexarch root, at the commencement of secondary growth; *px.*, three of the protoxylem-groups. That to the left is connected with the base of a rootlet. *x.*, *x.*, primary xylem; *c.p.*, conjunctive parenchyma; *ph.*, three phloëm-groups, alternating with the protoxylem; *cb.*, cambium, just beginning its activity opposite the phloëm-groups; *en.*, endodermis. × 100. C.N. 1631 (see pp. 736 and 739).

Fig. 21

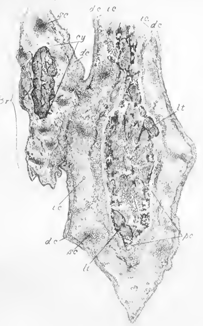


Fig 22

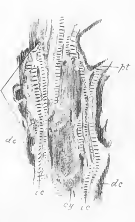


Fig 25.

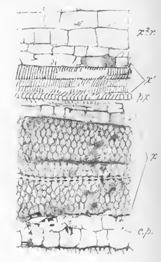


Fig 23.

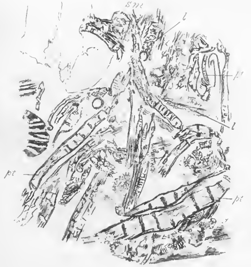
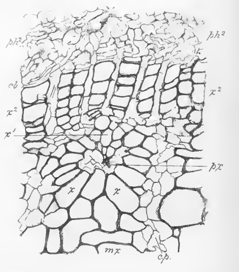


Fig. 24



Figs 21–25. Heterangium Grievii

PLATE 26.

Fig. 21. Transverse section through a young stem giving off a branch, *br.* *pc.*, pericycle of main stem, enclosing the stele; *l.t.*, *l.t.*, leaf-trace bundles; *i.c.*, inner cortex; *sc.*, sclerotic masses seen in both stem and branch; *d.c.*, outer cortex of stem and branch; *cy.*, stele of branch, with commencement of secondary wood. × 8. C.N. 1915N (Dulesgate) (see pp. 745 and 753).

Fig. 22. Somewhat oblique, longitudinal section of a stem, showing the bases of two petioles, *pt.*; the left-hand petiole is seen in nearly radial section. *cy.*, stele of stem; *i.c.*, inner cortex, which in both petiole and stem is marked by the transverse sclerotic bands; *d.c.*, outer, or *Dictyoxylon* cortex. × 2¼. C.N. 1286 (Burntisland) (see p. 754).

Fig. 23. Fragments of foliage from another section of the same block. Portions of petioles, *pt.*, of all sizes, are shown, characterized by the cortical structure. At *l.* are fragments of leaflets; *sm.*, a fern-sporangium. × 14. C.N. 1287 (Burntisland) (see p. 755).

Fig. 24. Part of a transverse section of a stem, showing one of the primary xylem-strands at the periphery of the stele. *px.*, protoxylem; *x.*, centripetal, $x.^1$, centrifugal, part of xylem; *mx.*, metaxylem, which extends through the whole interior of the stele; *c.p.*, conjunctive parenchyma; $x.^2$, secondary wood; *cb.*, cambium; $ph.^2$, secondary phloëm. × 200. C.N. 1293 (Burntisland) (see pp. 748 and 751).

Fig. 25. Radial section through the corresponding region of another stem, to show the mesarch structure of the xylem-strand. $x.^2r.$, ray belonging to the secondary wood. Other lettering as in previous figure. Note the well-preserved bordered pits of the centripetal xylem. × 200. C.N. 1266 (Burntisland) (see pp. 748 and 751).

Fig 26

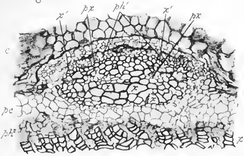


Fig. 27.

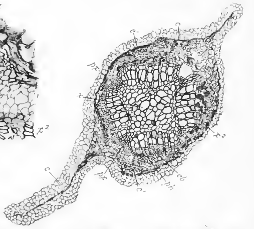


Fig 28

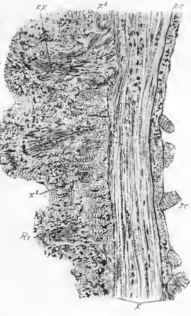
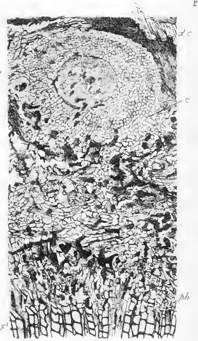


Fig. 29.



Figs 26–29. Heterangium Grievii

PLATE 27.

Fig. 26. Part of a transverse section of a stem, showing a collateral leaf-trace bundle, just separating from the stele. *px.*, *px.*, probable position of the protoxylem-groups; *x.*, centripetal, *x.'*, centrifugal, part of xylem of bundle; *ph.'*, its phloëm; *x.*², secondary wood of stem; *ph.*², phloëm; *pc.*, pericycle; c., inner cortex. × 70. C.N. 1253 (Burntisland) (see p. 750).

Fig. 27. Transverse section of a tetrarch root, probably belonging to *H. Grievii.* *px.*, *px.*, two of the four protoxylem-groups, at the corners of the massive primary wood; *x.*², secondary wood; *cb.*, cambium; *ph.*, phloëm; *c.'*, inner cortex; *c.*, outer cortex, or epidermal layer. × 40. C.N. 1915R (Dulesgate) (see p. 758).

Fig. 28. Radial section of a stem, bearing three adventitious roots, *Rt.* *r.x.*, xylem of root, connected with that of stem; *x.*², secondary wood of stem, chiefly developed near bases of roots, and partly seen in transverse section; *x.*, primary wood of stem; *pc.*, pericycle; *sc.*, sclerotic masses, the only remains of the cortex. × 15. C.N. 1915G (Dulesgate) (see p. 756).

Fig. 29. Part of transverse section of a stem, showing what is probably a young adventitious root (*Rt.*) enclosed in the cortex. The supposed root has a definite stele. c., its outer cortex, or epidermal layer; *d.c.*, part of the *Dictyoxylon* cortex of stem; *ph.*, phloëm; *x.*², secondary wood. × 50. C.N. 1915 (Dulesgate) (see p. 757.)

Fig 30.

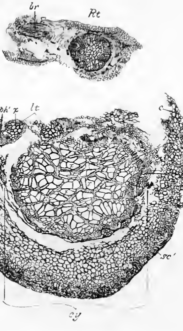


Fig. 31.

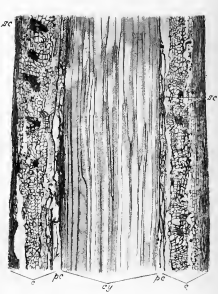


Fig 32.

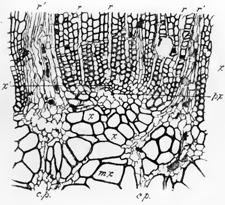
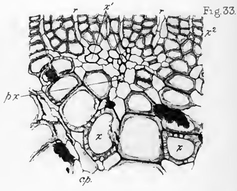


Fig. 33.



Figs 30 and 31, Heterangium sp
Figs. 32 and 33, Heterangium tiliæoides.

PLATE 28.

Figs. 30 and 31. *Heterangium sp.*

Fig. 30. Transverse section of stem. *cy.*, stele; *x.*, tracheides of the xylem which occupies the whole interior; *x.*², secondary wood, not much developed; *ph.*, remains of phloëm; *sc.'*, sclerotic nests in pericycle; c., cortex; *sc.*, sclerotic cortical mass; *lt.*, pair of leaf-trace bundles; in the left hand one, xylem, *x.*, and phloëm, *ph.'*, can be distinguished; *Rt.*, a tetrarch root, perhaps connected with the stem; *br.*, rootlet. × 18. C.N. 1304A (see p. 764).

Fig. 31. Part of the longitudinal section of the same specimen. Lettering as before. The scale is too small to show the details of the tracheides, which have crowded bordered pits. × 18. C.N. 1304B (see p. 764).

Figs. 32 and 33. *Heterangium tiliæoides.*

Fig. 32. Part of a transverse section of a stem, showing portions of the primary and secondary wood. *px*, protoxylem of one of the peripheral xylem-strands of the stele; *x.*, its centripetal, *x.'*, its centrifugal, primary xylem; *mx.*, metaxylem, which extends all through the interior of the stele; *c.p.*, conjunctive parenchyma; *x.*², secondary wood; *r.'*, *r.'*, the two principal rays, limiting the bundle; *r.*, *r.*, secondary rays. × 70. C.N. 1619 (see p. 760).

Fig. 33. Part of transverse section of another stem, showing mesarch xylem-strand more in detail. Lettering as before. Note the pitting on the walls of the primary tracheides. × 150. C.N. 1301 (see p. 760).

Fig 34

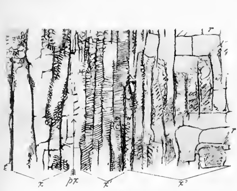


Fig 35

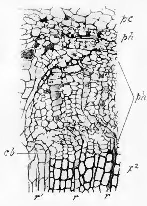


Fig.36

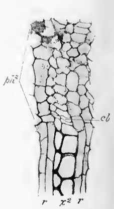


Fig 37

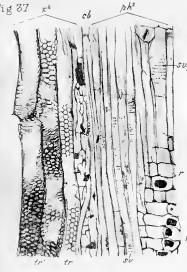


Fig 38A

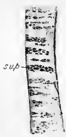
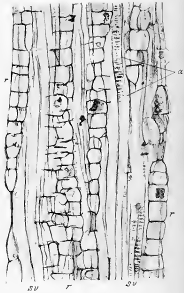


Fig 38.



Figs.34–38A Heterangium tiliæoides.

PLATE 29. *Heterangium tiliæoides.*

Fig. 34. Part of radial section of another stem passing through the corresponding region and showing the position of the protoxylem, *px.* (here much disorganized) in the xylem-strand. Lettering as in last two figures. × 150. C.N. 1628 (see p. 760).

Fig. 35. Another part of the same transverse section as fig. 32, to show cambium and phloëm. *x.*², secondary wood; *r.'*, principal ray; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*², secondary phloëm; *ph.*, primary phloëm; *pc.*, pericycle. × 70. C.N. 1619 (see p. 761).

Fig. 36. Small part of transverse section of another stem, specially good for cambium. *x.*², strand of secondary wood; *r.*, *r.*, secondary rays; *cb.*, cambium; *ph.*², secondary phloëm. × 150. C.N. 1302 (see p. 761).

Fig. 37. Part of the same radial section as fig. 34, to show developing wood, cambium, and phloëm. *x.*², secondary wood; *tr.'*, fully developed tracheides with bordered pits; *tr.*, developing tracheide with primordial pits only; *cb.*, cambium; *ph.*², secondary phloëm; *s.v.*, sieve-tube; *s.v.p.*, compound sieve-plate (also visible at other places); *r.*, secondary phloëm-ray. × 150. C.N. 1628 (see p. 761).

Fig. 38. Oblique longitudinal section through phloëm of another stem. *r.*, *r.*, phloëm-rays; *s.v.*, sieve-tubes; on several of the walls the sieve-plates are evident. × 150. C.N. 1304 (see p. 762).

Fig. 38A. Part of a sieve-tube enlarged from the previous section, at *a*, showing the sieve-plates, *s.v.p.* × 500. C.N. 1304 (see p. 762).